Relative Phase Dynamics in Motor-Respiratory Coordination

by

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ABSTRACT

Motor-respiratory coordination is the synchronization of movement and breathing during exercise. The relation between movement and breathing can be described using relative phase, a measure of the location in the movement cycle relative to the location in the breathing cycle. Stability in that relative phase relation has been identified as important for aerobic efficiency. However, performance can be overly attracted to stable relative phases, preventing the performance or learning of more complex patterns. Little research exists on relative phase dynamics in motor-respiratory coordination, although those observations underscore the importance of learning more. In contrast, there is an extensive literature on relative phase dynamics in interlimb coordination. The accuracy and stability of different relative phases, transitions between patterns, and asymmetries between components are well understood. Theoretically, motor-respiratory and interlimb coordination may share dynamical properties that operate in their different physiological substrates. An existing model of relative phase dynamics in interlimb coordination, the Haken, Kelso, Bunz model, was used to gain an understanding of relative phase dynamics in the less-researched motor-respiratory coordination. Experiments 1 and 2 were designed to examine the interaction of frequency asymmetries between movement and breathing with relative phase and frequency, respectively. In Experiment 3, relative phase stability and transitions in motor-respiratory coordination were explored. Perceptual constraints on differences in stability were investigated in Experiment 4. Across experiments, contributions relevant to questions of coordinative variability were made using a

dynamical method called cross recurrence quantification analysis. Results showed much consistency with predictions from an asymmetric extension of the Haken, Kelso, Bunz model and theoretical interpretation in the interlimb coordination literature, including phase wandering, intermittency, and an interdependence of perception and action. There were, however, notable exceptions that indicated stability can decrease with more natural frequency asymmetries and the connection of cross recurrence measures to categories of variability needs further clarification. The complex relative phase dynamics displayed in this study suggest that movement and breathing are softly-assembled by functional constraints and indicate that motor-respiratory coordination is a self-organized system.

DEDICATION

To those who have provided the most support and with whom celebrating this accomplishment will be most special, my wife and companion, Eve, and my parents, Marv and Molly.

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Relative Phase Dynamics in Motor-Respiratory Coordination

Motor-respiratory coordination, the synchronization of movement and breathing, occurs naturally during exercise. The relation between movement and breathing can be described using a collective measure called relative phase, the location in the cycle of one oscillator relative to the location in the cycle of the other. Despite the connection of relative phase to aerobic efficiency (e.g., Siegmund et al., 1999) and more complex coordination (Hessler & Amazeen, submitted), there has been little research on relative phase dynamics in motor-respiratory coordination. Theoretically, motor-respiratory coordination may share relevant properties with other types of coordination. The principle that similar dynamics operate in systems of different material substrate is known as dynamical similitude (Kelso, 1995). There is an extensive literature on relative phase dynamics in interlimb coordination, in which the components are limbs (arms, legs) or limb segments (e.g., fingers, hands) (e.g., Haken, Kelso, & Bunz, 1985; Kelso, 1984; Yamanishi, Kawato, & Suzuki, 1980). Capitalizing on dynamical similitude, principles and methodology from the interlimb coordination literature (Kelso, 1984; Kugler & Turvey, 1987) can be used to gain a further understanding of relative phase dynamics in the less-researched motor-respiratory coordination.

Aerobic Efficiency

There is increasing evidence in the motor-respiratory coordination literature of a connection between relative phase performance and aerobic efficiency. Walkers (Hill, Adams, Parker, & Rochester, 1988) and runners (Bramble & Carrier, 1983) tend to inhale with the contact of one of their heels to

the ground, and rowers (Bateman, McGregor, Bull, Cashman, & Schroter, 2006; Siegmund et al., 1999), after the blade of the oar meets the resistance of the water. The timing of those inhalations allows athletes to avoid inhaling when mechanical loading on the lungs is greatest. Loading occurs as a result of the vertical impulse generated from each foot striking the ground in walking and running, and compressions that occur during each forward reach, when the blade of the oar enters the water in rowing. Inhaling when mechanical loading on the lungs is low thereby accommodates deeper breathing, which increases oxygen uptake and improves the economy of performance (Cunningham, Goode, & Critz, 1975).

Across exercises, the number of movements produced per breath also locks into mostly smaller-integer, simple ratios (*m*:1) (e.g., 1:1, 2:1, 3:1) (Amazeen, Amazeen, & Beek, 2001; Bramble & Carrier, 1983; Mahler, Hunter, Lentine, & Ward, 1991). Other larger-integer, complex ratios (e.g., 5:3) are almost never performed by naïve participants, and are even difficult to facilitate via real-time feedback (Hessler, Gonzales, & Amazeen, 2010). Performance of smaller-integer, simple ratios during athletic performance has been associated with an increased ability to maintain consistent relative phase relations between movement and breathing (Bernasconi & Kohl, 1993; Bonsignore, Morici, Abate, Romano, & Bonsignore, 1998; Mahler, Shuhart, Brew, & Stukel, 1991). Daffertshofer, Huys, and Beek (2004) proposed a dynamical model of motor-respiratory coordination based on such findings from rowing. Through their modeling, they demonstrated that inhaling between periodic lung compressions should be achieved most effectively when movement and breathing lock into

smaller-integer, simple ratios because phase relations are less modulated by frequency variability of the components.

A steady supply of oxygen to the muscles is a general requirement for sustained aerobic activity (Bramble & Carrier, 1983). Stability in the coupling between movement and breathing has been identified as important for the maintenance of that steady oxygen supply (Bernasconi & Kohl, 1993; Garlando, Kohl, Koller, & Pietsch, 1985; Mahler, Shuhart, et al., 1991; van Alphen & Duffin, 1994). That is consistent with the high levels of entrainment observed between movement and breathing for expert runners (Bonsignore et al., 1998; McDermott, Van Emmerik, & Hamill, 2003), rowers (Siegmund et al., 1999), and manual wheelchair operators (Amazeen et al., 2001). Research on coordination between the limbs has shown that stability was higher at anchor points as opposed to away from anchor points (Byblow, Carson, & Goodman, 1994; Fink, Foo, Jirsa, & Kelso, 2000; Kudo, Park, Kay, & Turvey, 2006). Thus, anchoring between movement and breathing and between movements in other tasks may benefit performance through increased stability. Stability in the anchoring between movement and breathing is likely most critical in activities in which aerobic activity is most sustained like long-distance bicycling, running, and swimming (e.g., Bramble & Carrier, 1983).

The issues of stability and flexibility should be considered hand-in-hand. While stability may be generally important for performance, flexibility allows athletes to accommodate to changing performance demands. Previous studies have documented shifts between coordination patterns with increases in

movement frequency during running (Bramble & Carrier, 1983) and manual wheelchair propulsion (Amazeen et al., 2001), as well as intentional control over the patterns used to control gear shifts and even decoupling of movement and breathing during cycling (Garlando et al., 1985). Flexibility is necessary to avoid hyperventilation (Fabre et al., 2006) but is also of general importance across more typical frequencies of rhythmic exercise. A means of flexibility proposed by Garlando et al. (1985) is that the strength of coupling between movement and breathing should not be too high so that athletes can easily shift between the coordination patterns that are naturally available. Transitions between different relative phase patterns can, therefore, be considered adaptive.

More Complex Coordination

The connection between relative phase performance and aerobic efficiency underscores the importance of learning more about the relative phase dynamics between movement and breathing. An understanding of those dynamics is also important because relative phase preferences can influence even more complex coordination (Hessler & Amazeen, submitted; for examples from interlimb coordination, see Zanone & Kelso, 1992a, 1992b). In one study, participants were instructed to coordinate forward-backward arm movement about the shoulder joint with breathing (Hessler & Amazeen, submitted). With the assistance of visual displays, participants were asked to perform larger-integer, complex ratios (e.g., 5:3) and smaller-integer, simple ratios (e.g., 3:1). To determine whether or not movement and breathing tended to anchor in certain relative phase patterns, relative phase at time t and time $t + \tau$ (after a time delay equivalent to about

¼ cycle) were plotted against each other. Those lagged return plots, produced for representative 5:3 (left panel) and 3:1 (right panel) trials, are depicted in Figure 1.

insert Figure 1 about here.

For idealized ratio performance, the change from relative phase$_t$ to relative phase$_{t+\tau}$ would be a constant, resulting in data points lying along the dashed lines. Real data were noisier, as was evident by the spread of points in the lagged return plots. For the 5:3 trial (left panel), data clustered at 0° relative phase$_t$ and relative phase$_{t+\tau}$, and ±180° relative phase$_t$ and relative phase$_{t+\tau}$. Those results indicated actual behavior was different from the difficult ratios participants were instructed to perform. Described with respect to prominent landmarks, during larger-integer, complex ratio trials, forward-most arm movements tended to coincide directly with either maximum exhalations or maximum inhalations longer than with other phases of the breathing cycle. Those relative phase patterns are corollaries to the stable relative phase preferences in interlimb coordination (e.g., Yamanishi et al., 1980). An interesting parallel between motor-respiratory coordination and performance in interlimb coordination is that errors committed by skilled pianists often result from tendencies to perform stable relative phase patterns between the left and right hands (Shaffer, 1980). Together, those results reflect the similarity between rhythmic performance in exercise and music.

By comparison, data points were in the vicinity of the dashed line for the 3:1 trial (see Figure 1, right panel), which indicates that differential attraction of

arm movement to certain phases of the breathing cycle was not observed and performance approximated that expected for the idealized smaller-integer, simple ratio. As a reminder, such ratios are observed most often across exercises (e.g., Amazeen et al., 2001; Bramble & Carrier, 1983). A possible reason for the observed difference in ratio performance was the phase relations with breathing at prominent movement landmarks. For larger-integer, complex ratios, the relative phase relations required for idealized performance at those landmarks varied considerably, whereas for smaller-integer, simple ratios, there were always stable relative phase relations at those landmarks. Thus, to gain insight into even more complex motor-respiratory behavior, it is necessary to further understand relative phase dynamics.

Toward a Model of Relative Phase Dynamics

Beyond the literature discussed, there is little else known about relative phase dynamics in motor-respiratory coordination. The parallel with piano playing (Shaffer, 1980) is one of many connections between motor-respiratory coordination and interlimb coordination. Some background on relative phase dynamics and theory in interlimb coordination is necessary to develop motor-respiratory coordination experiments. To examine relative phase performance, researchers presented participants with a series of relative phase patterns using a visual metronome (Tuller & Kelso, 1989; Yamanishi et al., 1980; Zanone & Kelso, 1992a, 1992b, 1997). Participants mimicked the presented relative phase patterns between taps of their left and right hands. Inphase, when homologous muscles flex and extend together, and antiphase, when homologous muscles flex

and extend alternately, were performed with greater accuracy and stability than other relative phases (e.g., Yamanishi et al., 1980; for evidence from an alternate paradigm see Kelso, 1984). Performance of more difficult relative phases, like the gallop in which one hand led the other by ¼ cycle, was also drawn toward inphase and antiphase.

There are very many neural, muscular, metabolic, and perceptual constraints (Kelso, Schöner, Scholz, & Haken, 1987; Schöner, Haken, & Kelso, 1986) underlying performance in both interlimb coordination and motor-respiratory coordination that operate over different time scales. Those coordinative systems are, by definition, structurally complex. The implication of that structural complexity is that any one of those underlying components has the potential to affect the stability of relative phase performance (Amazeen, Da Silva, & Amazeen, 2008; Kelso, 1995; Li, Levin, Carson, & Swinnen, 2004; Park, Collins, & Turvey, 2001). To provide a coherent account of coordination describing each of those components and their many nonlinear interactions would be an impossible task (Bernstein, 1967). There are too many degrees of freedom for which to account. An alternate strategy, the one employed in the modeling of relative phase dynamics (Haken et al., 1985), is to provide a description of behavior at a more macroscopic level.

The theoretical underpinnings in the modeling of relative phase dynamics were derived from a theoretical approach and modeling strategy known as synergetics (Haken, 1983), originally developed to describe the physics of lasers. In synergetics, the relation between two parameters is examined. Variation in a

control parameter produces a specific pattern of change in an order parameter. A particularly relevant control parameter in coordination research is movement frequency (Haken et al., 1985; Kelso, 1984; Scholz & Kelso, 1989; Schöner et al., 1986). Initial increases in frequency produce incremental changes in relative phase until suddenly, relative phase changes dramatically (Kelso, 1984). The order parameter, relative phase, emerges through cooperation of the very many complex and interconnected parts of the system and is, thus, considered a collective variable (Haken et al., 1985). Although it reflects the behavior of each underlying part, relative phase is a comparatively simpler description. The higher-level order parameter also governs or slaves the behavior of lower-level components upon its formation, completing a kind of circular causality.

The principles of synergetics are not at all unique to coordination (Haken, 1983). They are necessarily general. The foundational example, which I introduce to help explicate the theory, is Rayleigh-Bénard convection in which a fluid is heated from below and cooled from above (Haken, 1983, 1996; Kelso, 1995; Velarde & Normand, 1980). The control parameter in this system is the difference in temperature between the lower surface and the upper surface (ΔT) and the order parameter is the qualitative behavior of the fluid molecules. When ΔT is small, heat is dissipated through relatively independent motions of the individual fluid molecules (conduction). In contrast, when ΔT reaches a critical value, heat is dissipated through a dramatically different physical regime. A rolling motion suddenly develops in the fluid (convection rolls). For a relevant and interesting

meteorological example of convection rolls, consider the formation of cloud streets—lines of cumulus clouds—on a hot summer's day (Kuo, 1963).

An essential characteristic of Rayleigh-Bénard convection and any other synergetic system is that they be open. In terms of Rayleigh-Bénard convection, there was an interaction with the environment: an input of energy in the form of heat (Kelso et al., 1987; Schöner et al., 1986). Although that energy input came from outside the system, metabolic systems like motor-respiratory coordination and interlimb coordination are open to both internal and external energy input (Kelso, 1995). Without some form of energy exchange, it is impossible for a system to maintain structure (Babloyantz, 1986). The tendency will be for the system to drift toward thermodynamic equilibrium (Turing, 1952). In the case of the fluid in the Rayleigh-Bénard example, the pattern across fluid molecules would be entirely homogeneous at a thermodynamic equilibrium. From the synergetics perspective (Haken, 1983), systems of interest (most real-world systems) are far from that thermodynamic equilibrium. Open, far-from-equilibrium systems are the types of systems in which interesting patterns and structure arise (Kelso et al., 1987).

Modeling Relative Phase Dynamics

Relative phase dynamics in interlimb coordination were mathematically formalized in the HKB model, so named after the researchers that developed the model: Haken, Kelso, and Bunz (1985). In the HKB model, the collective order parameter, relative phase, is defined over quantities derived from two component oscillators ($\phi = \theta_1 - \theta_2$), where θ_i is the phase angle of each oscillator. The

oscillators in the original description of the model were the index fingers of the left and right hands. However, the variable relative phase applies to any pair of oscillators. That is, relative phase can be defined across the left and right hands (e.g., $\phi = \theta_{left} - \theta_{right}$) or movement and breathing (e.g., $\phi = \theta_{movement} - \theta_{breathing}$). The relative phase dynamics are then described by the following motion equation (Haken et al., 1985; Kelso, DelColle, & Schöner, 1990),

$$\dot{\phi} = \Delta\omega - a\sin(\phi) - 2b\sin(2\phi) + \sqrt{Q}\zeta_t \quad (1),$$

where the derivative of relative phase, $\dot{\phi}$, changes as a function of relative phase, ϕ, a detuning term, $\Delta\omega$, the strength of coupling between oscillators, b/a, and a Gaussian white noise process, ζ, of strength Q, that arises from the system's underlying structural complexity. In practice, ζ is a series of stochastic perturbations that result in a distribution of relative phase values centered on the mean relative phase. More generally, the HKB model has a deterministic component ($\Delta\omega$, a, b) and a stochastic component (ζ).

An increase in the value of the control parameter b/a reflects an increase in movement frequency in interlimb coordination (e.g., Kelso, 1984). Figure 2 depicts Equation 1 for a comfortable frequency ($b/a = 1$; solid line) and a fast frequency ($b/a = 0.25$; dashed line) with $\Delta\omega = 0$. Stable attractors are indicated by negatively-sloped zero crossings and unstable repellors by positively-sloped zero crossings. The strength of attraction or repulsion increases with the slope magnitude λ, the value of $d\dot{\phi}/d\phi$ evaluated at the relative phase (Schöner et al., 1986). For the comfortable frequency, there is an attractor at inphase (0^o), a less

stable attractor (shallower negative slope) at antiphase (±180º), and repellors at the gallop patterns (+90º: right-leads-left; -90º: left-leads-right). For the fast frequency, antiphase becomes a repellor, leaving only the inphase attractor, and accounting for the often observed antiphase to inphase transition (e.g., Kelso, 1984).

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insert Figure 2 about here.

Asymmetry between the components involved in coordinative activity is one underlying feature that influences the synergetics of coordination. In reality, attraction to the perfect inphase and antiphase patterns is really only a property of symmetric oscillators like two index fingers (Kelso, 1984). Attraction to inphase and antiphase may be exhibited but offset by physical differences between the components associated with their natural frequency asymmetry. A prominent example of an asymmetric system is coordination between the arms and legs (Jeka & Kelso, 1995; Kelso & Jeka, 1992). Specifically, the natural frequency of arm movement is much faster than that of leg movement, the consequence of which is a fixed point shift (a shift in attractor location). Fixed point shift is the arithmetic difference ($\phi - \psi$) between the predicted, ϕ, and intended, ψ, relative phase. Compared to perfect inphase and antiphase patterns, the faster frequency component, arm movement, tends to lead the slower frequency component, leg movement. The detuning term, $\Delta\omega$, added to the HKB model in order to account for fixed point shifts (Kelso et al., 1990), has been equated with the arithmetic

difference ($\omega_2 - \omega_1$) between the natural frequencies of the component oscillators (e.g., Amazeen, Amazeen, & Turvey, 1998a; Kelso & Jeka, 1992).[1] There is, therefore, a direct link between fixed point shift and frequency asymmetry in the model.

Figure 3 depicts Equation 1 for no frequency asymmetry ($\Delta\omega = 0$; solid line) and a negative frequency asymmetry ($\Delta\omega = -1$; dashed line) with b/a = 1. The negative $\Delta\omega$ does not change the shape of the motion equation function; it simply shifts the function down. In the model, frequency asymmetry causes the predicted attractor locations to shift. For a negative $\Delta\omega$ (dashed line), the negatively-sloped zero crossings shift to the left (i.e., there is a negative phase shift). The predicted shift from antiphase ($\pm 180^o$) is larger than the predicted shift from inphase (0^o). Note how the horizontal distance between the negatively-sloped zero crossings for $\Delta\omega = 0$ (solid line) and $\Delta\omega = -1$ (dashed line) is larger for antiphase than inphase. Although it is subtle in the model, the slopes at the new zero crossings are slightly more shallow. Those new attractor locations are, therefore, predicted to be less stable.

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insert Figure 3 about here.

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[1] $\Delta\omega$ is subject to additional interpretation when different natural component frequencies form a constant ratio (e.g., 2:1 = 4:2; Collins, Sternad, & Turvey, 1996; Sternad, Collins, & Turvey, 1995). That special case does not apply in motor-respiratory coordination because the natural breathing frequency is not subject to safe manipulation.

A more comprehensive illustration of the fixed point shift (top panels) and variability (bottom panels) predictions of the HKB model are depicted in Figure 4. To generate the predictions, several values of $\Delta\omega$ were used. The exact predictions regarding the influence of $\Delta\omega$ on performance depend on relative phase mode (left panels) and frequency (right panels). The wrist-pendulum paradigm (e.g., Kugler & Turvey, 1987; Rosenblum & Turvey, 1988; Turvey, Rosenblum, Schmidt, & Kugler, 1986) was designed to allow researchers to examine those predictions experimentally in interlimb coordination. Of particular significance is the ability to experimentally control frequency asymmetry: longer, heavier pendulums have slower natural frequencies than shorter, lighter pendulums (Kugler & Turvey, 1987; Rosenblum & Turvey, 1988). In general, the results obtained using the wrist-pendulum paradigm are consistent with predictions of the HKB model. Predictions of the HKB model are easily clarified by discussing the results obtained in that previous wrist-pendulum work.

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insert Figure 4 about here.

In a seminal wrist-pendulum study, Rosenblum and Turvey (1988) instructed participants to intentionally move hand-held pendulums at a common speed and in an antiphase relation. The results of that study were consistent with the predictions depicted as dashed lines in the left panels of Figure 4. A perfect antiphase relation ($\phi - \psi = 0$) was achieved only when pendulums that shared the same natural frequency were held in the left and right hands (frequency

asymmetry = 0). When the pendulums had different natural frequencies, the faster pendulum led the slower pendulum ($\phi - \psi \neq 0$). Negative versus positive fixed point shifts depended on whether the fast pendulum was held in the left ($\phi - \psi < 0$) or right ($\phi - \psi > 0$) hand. The faster pendulum lead was amplified when the difference in the natural frequency characteristics of the pendulums increased (a positive slope in the top left panel). Along with that shift, the variability of performance also increased (bottom left panel). Those general fixed point shift and variability finding have received much empirical support in the interlimb coordination literature (e.g., Amazeen et al., 1998a; Amazeen, Sternad, & Turvey, 1996; Schmidt, Shaw, & Turvey, 1993; Sternad, Amazeen, & Turvey, 1996; Sternad, Turvey, & Schmidt, 1992; Turvey et al., 1986).

When a sufficiently wide range of frequency asymmetries was explored, the different predictions for inphase and antiphase performance were supported (see Figure 4; top left panel). Shifts in performance from antiphase (dashed line) were larger than from inphase (solid line) (Sternad et al., 1996; Treffner & Turvey, 1995; but not in Schmidt et al., 1993; Turvey et al., 1986). Consistent with the predictions in the top right panel of Figure 4, a higher movement frequency (dashed line) magnified the shifts in attractor location relative to the lower movement frequency (solid line), particularly when there were large natural frequency differences between components (i.e., a discontinuous shift at larger $\Delta\omega$; Amazeen et al., 1996; Schmidt et al., 1993; Sternad et al., 1992). Consistent with the predictions depicted in the bottom panels of Figure 4, fixed point shifts were also coordinated with an increase in relative phase variability (Amazeen et

al., 1996, 1998a; Schmidt et al., 1993; Sternad et al., 1992, 1996; Treffner & Turvey, 1995; Turvey et al., 1986). Those results from interlimb coordination highlight useful areas of exploration in motor-respiratory coordination.

Motor-Respiratory Coordination and Frequency Asymmetry

Corollaries to the inphase and antiphase patterns observed in interlimb coordination exist in motor-respiratory coordination. In the lagged return plot for the 5:3 trial (see Figure 1, left panel) was evidence of two stable relative phase patterns (Hessler & Amazeen, submitted). Preliminary evidence suggests that participants tend to spontaneously adopt one of those relative phases more often than the other (Bateman et al., 2006; Hessler & Amazeen, 2009; Siegmund et al., 1999). Given that no other evidence is available, I hypothesize that the often-adopted pattern, coordination of forward-most movements with maximum exhalations, is inphase, and the less-adopted pattern, coordination of forward-most movements with maximum inhalations, is antiphase. At present, it is not clear whether the same relative phase dynamics displayed within the motor subsystem (interlimb coordination) will also be displayed between bodily subsystems (motor-respiratory coordination). Exploring the relationship between interlimb coordination and motor-respiratory coordination in more depth is central to this dissertation.

Some of the prominent relative phase dynamics exhibited in interlimb coordination were shifts in attractor location and changes in variability with frequency asymmetry. Although it has received some mention (Temprado et al., 2002), there has been little research on the impact of frequency asymmetries in

motor-respiratory coordination. The effects of those asymmetries are important to study in motor-respiratory coordination, however, because different frequency asymmetries are exhibited between movement and breathing across a range of human activities (e.g., Amazeen et al., 2001; Bramble & Carrier, 1983; Garlando et al., 1985; Mahler, Hunter, et al., 1991). Temprado et al. (2002) instructed participants to maintain different relative phase patterns in a 1:1 frequency relation. The tendency was for the oscillator of slower natural frequency, breathing, to lead the oscillator of faster natural frequency, wrist movement. A similar result was expected in the current study, although such a prediction is opposite the interlimb coordination results outlined in which the faster pendulum led the slower pendulum (Amazeen et al., 1996, 1998a; Rosenblum & Turvey, 1988; Schmidt et al., 1993; Sternad et al., 1992, 1996; Turvey et al., 1986).

For wrist-pendulum studies (e.g., Kugler & Turvey, 1987), frequency asymmetries were achieved by having participants coordinate pendulums of different lengths and masses. That is fundamentally different from motor-respiratory coordination because the magnitude of the frequency asymmetry was induced rather than existing. The frequency ratios exhibited across different exercises demonstrate that the natural frequency of most movements is much faster than that of breathing (e.g., Amazeen et al., 2001; Garlando et al., 1985; Mahler, Hunter, et al., 1991). In contrast, the natural frequencies of the left and right hands are effectively the same. Given the naturally asymmetric state between movement and breathing, the relation between asymmetry and variability might be different for motor-respiratory coordination than for wrist-pendulum

coordination. Rather than increasing, relative phase variability could decrease with larger frequency asymmetry (changing the U-shaped functions in the bottom panels of Figure 4 to inverted U-shaped functions), as motor-respiratory coordination approaches its more natural state. In addition, because breathing frequency is generally slower than movement frequency (i.e., $\Delta\omega$ is negative), the full inverted U-shaped function and corresponding fixed point shift predictions are unlikely to be manifested in motor-respiratory coordination.

Classifying Variability

Understanding how differences in variability arise has been a major focus in recent years (Kudo et al., 2006; Pellecchia, Shockley, & Turvey, 2005; Richardson, Schmidt, & Kay, 2007; Shockley & Turvey, 2005, 2006). Traditionally, changes in variability have been ascribed to differences in attractor strength (e.g., Haken et al., 1985). From that perspective, changes in variability are assumed to be fully deterministic (Riley & Turvey, 2002). For example, consider coordination of the hands in an inphase pattern. One aspect of that performance is the simultaneous contraction of homologous muscle groups. Assuming determinism, the specific contribution of homologous muscle firing to the variability of inphase performance could be established in a 1:1 fashion. As Richardson et al. (2007) noted, however, differences in attractor strength are sometimes only visible when noise perturbs the system away from an attractor. That is, some random input of variability is required for a system to exhibit pattern formation and change.

In previous work, attractor strength has been evaluated using the standard deviation of relative phase (SDϕ) (Amazeen, Amazeen, & Turvey, 1998b; Amazeen et al., 1996; Schmidt et al., 1993; Sternad et al., 1996). However, SDϕ is a function of both attractor strength, indexed as λ, and the amount of stochastic noise perturbing coordination, indexed as Q (Richardson et al., 2007; Schöner et al., 1986),

$$SD\phi = \sqrt{\frac{Q}{2|\lambda|}} \qquad (2).$$

Observed changes in SDϕ over various experimental manipulations are, therefore, a function of changes in λ, Q, or both λ and Q (Kudo et al., 2006; Pellecchia et al., 2005; Richardson et al., 2007). Distinguishing between those different components is critical to understanding how differences in coordinative variability and susceptibility to transitions arise.

In most examinations of coordination to date, the important stochastic component of the HKB model was assumed to be constant (e.g., Haken et al., 1985). That was due, in part, because measures did not exist to differentiate between attractor strength and noise. More recently, that assumption has been empirically examined (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005, 2006) using a dynamical analysis procedure called cross recurrence quantification analysis (e.g., Shockley, Butwill, Zbilut, & Webber, 2002) designed to reveal similarities in the structure of two embedded time series. In interlimb coordination, two cross recurrence quantification analysis measures, MAXLINE and %REC, have been shown to index λ and Q, respectively

(Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005, 2006). That is because MAXLINE is a measure of the amount of time a pattern can be maintained, and %REC, a measure of shared activity irregardless of patterning. The details of those measures will be addressed in the calculations and dependent measures subsection of Experiment 1.

Demonstrating that not all manipulations result in deterministic changes alone, an increase in metronome variability (an introduction of perceptual fluctuations), increased the magnitude of noise observed for different patterns of interlimb coordination (Richardson et al., 2007). A similar result was observed for concurrent cognitive activity like mental arithmetic (Pellecchia et al., 2005), and word encoding and retrieval (Shockley & Turvey, 2005, 2006). Such influences on noise are hypothesized to result from neural, muscular, metabolic, and perceptual activity indirectly involved in the formation of any movement pattern (Rosenblum & Turvey, 1988). Metronome variability and concurrent cognitive activity were, therefore, assumed to be influences from outside coordination's immediate frame of reference.

Not all changes in deterministic and stochastic aspects of variability were so orthogonal. Although the magnitude of change in attractor strength was larger than in noise, attractor strength decreased and noise increased when movement frequency increased (Richardson et al., 2007). Differences in the frequency characteristic of pendulums also resulted in a decrease in attractor strength and an increase in the magnitude of noise relative to more symmetric pairs (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005). Moreover, changes

in MAXLINE and %REC cannot be considered completely orthogonal because shared patterning implies shared activity. That is, MAXLINE and %REC are correlated. Some attention to differences in the magnitude of changes in those components is, therefore, important in distinguishing λ and Q, although no guidelines have been provided in the literature. I will use MAXLINE and %REC in an effort to distinguish between changes in attractor strength and noise in motor-respiratory coordination for the first time.

Summary and Outline

The initial experiments in this dissertation were designed to gain a better understanding of the impact of frequency asymmetries on motor-respiratory coordination. Frequency asymmetry was explicitly manipulated in a manner consistent with the wrist-pendulum paradigm (Kugler & Turvey, 1987; Rosenblum & Turvey, 1988; Turvey et al., 1986). In the wrist-pendulum paradigm, natural pendulum frequencies were manipulated by varying their length and mass and performance was examined for each steady state condition. Although the natural frequency of breathing is not subject to safe manipulation, the natural frequency of leg movement is. To create different frequency asymmetries between movement and breathing, I manipulated the natural frequency characteristics of leg movement through the use of ankle weights. The natural frequency of leg movement was expected to decrease with increases in mass, more closely approximating the natural breathing frequency. That is, as the mass attached to the ankle increases, $\Delta\omega$ should decrease.

A pilot experiment was first performed, which confirmed the efficacy of that frequency asymmetry manipulation and indicated that leg movement frequency would change with different masses. Frequency asymmetry has been shown to interact with other variables in interlimb coordination including relative phase mode (e.g., Sternad et al., 1996; Treffner & Turvey, 1995) and oscillation frequency (e.g., Amazeen et al., 1996; Schmidt et al., 1993; Sternad et al., 1992). To explore those interactions in motor-respiratory coordination, frequency asymmetry and relative phase mode were manipulated in Experiment 1, and frequency asymmetry and oscillation frequency were manipulated in Experiment 2. In both experiments, the steady state paradigm advanced by Kugler and Turvey (1987) was employed to explore those interactions with a high degree of experimental control. The results were intended to provide insights into particular variables that influence more complex performance during motor-respiratory coordination. Later experiments were designed to directly examine more complex performance and perceptual constraints on differences in stability.

Experiment 1: Frequency Asymmetry and Relative Phase

In Experiment 1, participants were instructed to perform inphase and antiphase patterns between leg movement and breathing with ankle weights attached to the right ankle. The effect of frequency asymmetry on relative phase accuracy was expected to be consistent with observations in interlimb coordination and predictions of the HKB model (Amazeen et al., 1996, 1998a; Rosenblum & Turvey, 1988; Schmidt et al., 1993; Sternad et al., 1992, 1996; Turvey et al., 1986), except that the slower frequency component, breathing, was expected to lead the faster frequency component, leg movement (Temprado et al., 2002). Predictions regarding the accuracy of relative phase performance were derived from the HKB model (see Equation 1) and are presented in the top panel of Figure 5. To generate the predictions, several negative values of $\Delta\omega$ were used for the required inphase (solid line) and antiphase (dashed line) patterns. Constant error predictions were determined by taking the arithmetic difference ($\phi - \psi$) between the predicted detuned relative phase, ϕ, and the required relative phase, ψ.

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insert Figure 5 about here.

Because only negative $\Delta\omega$ were used, predicted shifts in attractor location are in the negative direction. That is, the predicted relative phase under asymmetric conditions is smaller than the required relative phase. Breathing was expected to lead movement. As $\Delta\omega$ increases, those shifts become more negative.

With a reduction in mass attached to the ankle (faster leg movement yields a larger frequency asymmetry with breathing), breathing was expected to further lead movement. For a given $\Delta\omega$, those shifts are more negative for antiphase than inphase. The amount that breathing leads movement was expected to be larger for antiphase than inphase performance, particularly at larger $\Delta\omega$.

In interlimb coordination, the effects of relative phase mode and frequency asymmetry on constant error were more subtle than on variable error (Amazeen et al., 1998a; Sternad et al., 1996). Movement and breathing were expected to be sufficiently detuned for effects on both constant error and variable error to be observed. Predictions regarding variable error are presented in the bottom panel of Figure 5. The variability of relative phase performance was expected to be higher for antiphase than inphase performance in motor-respiratory coordination. As outlined in the introduction, because of the natural frequency asymmetry between movement and breathing (e.g., Bramble & Carrier, 1983; Garlando et al., 1985), the relation between frequency asymmetry and the variability of relative phase performance was expected to be opposite that in wrist-pendulum studies (e.g., Rosenblum & Turvey, 1988). Motor-respiratory coordination was expected to be less variable, not more variable, at larger $\Delta\omega$.

With regard to the nature of changes in the variability of performance, differences resulting from relative phase mode have been hypothesized to result from intricacies directly involved in the formation of each coordination pattern (Riley & Turvey, 2002), like the specific pattern of activation of homologous muscle groups. Consistent with that hypothesis, relative phase mode influenced

attractor strength not noise in interlimb coordination (Richardson et al., 2007). Therefore, in the current study, MAXLINE should be lower for antiphase than inphase performance, while %REC should remain about the same. In contrast, frequency asymmetry has been hypothesized to increase the degrees of freedom both directly (e.g., pattern of homologous muscle activation) and indirectly (e.g., neuromotor noise associated with basic metabolic functions) involved in coordination (Fuchs & Kelso, 1994; Riley, Santana, & Turvey, 2001; Riley & Turvey, 2002). Reflecting such changes, MAXLINE and %REC decreased with increasing frequency asymmetry in interlimb coordination (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005). In the current study, the predictions were opposite, again, to reflect the natural frequency asymmetry between movement and breathing. MAXLINE and %REC were expected to increase with increasing frequency asymmetry.

Method

Participants

Nineteen participants (5 men, 14 women; 18–23 years old) received credit toward their introductory psychology course in exchange for their participation. The participants had full use of their legs and hips, were not experiencing any respiratory difficulties, did not smoke, and had normal or corrected to normal vision. All participants were treated in accordance with the ethical principles of the American Psychological Association.

Apparatus

Task characteristics. Figure 6 depicts the task performed. Each participant stood with the left foot on a 5 cm concrete block so that the right foot was slightly elevated to discourage contact with the ground. Participants supported themselves in an upright stance by holding onto height-adjustable bars with the hands. They were instructed to maintain an upright posture throughout each trial and not to shift the hands during trials. Participants swung the right leg forward and backward in the sagittal plane at a self-selected amplitude. Leg movement was used, as opposed to other limb movements (e.g., arm or finger), because it has the lowest natural frequency that is closest to the natural breathing frequency. Movement was constrained with a knee restraint to ensure rotation of the hip joint only and that movement involved the whole leg. Ankle weights of 1 kg (largest $\Delta\omega$), 3 kg, or 5 kg (smallest $\Delta\omega$) mass were attached to the right ankle to achieve different frequency asymmetries. Each ankle weight was 33 cm long and 15 cm high. Two Velcro straps secured each weight tightly around the ankle. Ten pockets on each ankle weight were filled with lead shot to achieve the required mass. Lead shot was distributed evenly around the ankle so that the leg was not unequally loaded. To avoid additional loading of the leg and unequal loading for different participants, the right shoe was removed. The oscillation frequency for movement and breathing was specified using an auditory metronome. Participants were instructed to select the point in each cycle to synchronize with metronome tones.

insert Figure 6 about here.

Data collection. Infrared emitters were attached to a rigid piece of wood and secured with Velcro to the right side of the knee brace. Movement was recorded using an Optotrak/3020 (Northern Digital, Waterloo, Canada). The Optotrak was positioned 2.5 m to each participant's right side, so that the emitters were not occluded at maximum forward and backward excursions of the leg. Breathing was recorded with a pneumotachometer (Hans Rudolph, Kansas City, MO) that samples airflow using a differential pressure method. The pneumotachometer was attached to a facemask worn over the nose and mouth. Movement and breathing data were sampled at 50 Hz and collection of those data was synchronized using an Optotrak Data Acquisition Unit.

Procedure

Before the experimental manipulation, baseline estimates of preferred frequency were obtained. For each baseline trial, the experimenter emphasized that the task should be performed at the most comfortable rhythm, as if it could be done all day (e.g., Kelso, 1984). On separate trials (order counterbalanced), each participant was instructed to swing the right leg forward and backward or to breathe in and out through the mouth. Estimates of movement frequency and loaded breathing frequency were obtained in one trial. An estimate of the resting breathing frequency was obtained in the other trial. Immediately following, baseline trials were performed for each mass condition (order randomized): 1 kg

(largest Δω), 3 kg, or 5 kg (smallest Δω). Each participant was instructed to swing the right leg forward and backward at the most comfortable rhythm. Estimates of movement frequency and loaded breathing frequency were obtained for each mass condition. All baseline trials were 60 s in length.

For experimental trials, participants were instructed to exhale with forward movements and inhale with backward movements (inphase) or inhale with forward movements and exhale with backward movements (antiphase). The order of presentation was counterbalanced. There were two 60 s experimental trials per relative phase pattern with each mass (order randomized): 1 kg (largest Δω), 3 kg, and 5 kg (smallest Δω). Duplicate trials were collected to ensure there was at least one analyzable trial per condition. All trials were performed at a prescribed metronome frequency of 0.54 Hz (the average preferred frequency during pilot testing). Participants were instructed to complete both one full movement cycle and one full breathing cycle per metronome tone. A minimum 30 s rest was provided between each trial to minimize fatigue. More rest was provided upon request.

Calculations and Dependent Measures

Data reduction and pre-processing. The top panels of Figure 7 depict 20 s samples of raw movement (left panel) and breathing (right panel) time series for a single participant who was performing the inphase pattern. As is typical, the breathing data were noisier. Movement and breathing data were filtered using a low-pass Butterworth filter with a cut-off frequency of 25 Hz. Filtering reduces the effect of high frequency measurement error on data analysis and has been

recommended for use in cross recurrence quantification analysis (Richardson et al., 2007). The initial 7 s of each trial was excluded from the analysis to account for a settling-in period. Filtered movement and breathing data were on different scales. It is standard in cross recurrence quantification analysis procedures to convert data to the same scale. While use of maximum-distance rescaling is typical, such rescaling can produce undesirable results if there are outliers. Because brief transients were sometimes present, especially in the breathing data, mean-distance rescaling was used.

insert Figure 7 about here.

Frequency. Movement and breathing frequencies were calculated by dividing the 50 Hz sampling rate by the difference between successive movement maxima (forward-most position of leg movement) and successive inhalation maxima, respectively. Movement and inhalation maxima were used because they were well-defined. Calculating frequency at those landmarks reduces the vulnerability of estimates to temporal measurement error. The mean frequency and variable error of frequency (*SD* frequency) were calculated from those cycle-by-cycle estimates. A cycle-by-cycle frequency ratio estimate was also calculated by dividing movement frequency by breathing frequency at the location of each inhalation maximum.

Continuous relative phase. Derivatives of the filtered movement and breathing data were calculated to obtain velocity time series. The filtered

movement and breathing data were plotted against their respective velocity time series to create phase portraits. Continuous relative phase could not be calculated from some of the initial phase portraits because of amplitude variation across cycles. Maxima and minima of position and velocity for each cycle were, therefore, used to normalize the data to the unit circle. The middle panels of Figure 7 depict phase portraits for movement (left panel) and breathing (right panel), corresponding to the same 20 s depicted in the top panels. The resulting phase portraits exhibited some pinching (a higher density of data points) at the locations used to normalize but such normalization was necessary to estimate relative phase. Breathing phase portraits also showed some deviation from circularity but phase angles were calculable, albeit leaving a footprint on relative phase (i.e., periodicity). The continuous phase angles of movement, $\theta_{movement}$, and breathing, $\theta_{breathing}$, were calculated. Continuous relative phase was the difference between the movement and breathing phase angles ($\theta_{movement} - \theta_{breathing}$). The bottom panel in Figure 7 depicts continuous relative phase, as calculated from the corresponding phase portraits. That measure and others derived from it were sensitive to experimental manipulations. Measures of accuracy (constant error) and variability (variable error) were calculated from continuous relative phase. Constant error was the average difference between the performed, ϕ, and intended, ψ, relative phase ($\phi - \psi$). Positive constant error indicated that movement led breathing and negative constant error indicated that breathing led movement. For the data in Figure 7, breathing generally led movement. Variable error was SDϕ.

Cross recurrence quantification analysis. Cross recurrence quantification analysis (Shockley et al., 2002; Zbilut, Giuliani, & Webber, 1998) was used to reveal similarities in the structure of reconstructed attractors for movement and breathing[2]. Cross recurrences, or overlapping data points, from the reconstructed movement and breathing attractors were determined. As is normal for loosely coupled systems, few data points are likely to overlap directly. Therefore, a radius around each point was selected because it represents a more liberal inclusion criterion. Other data points that fell within that radius were considered cross-recurrent. The number of cross-recurrent points varies with radius size. A radius of 21% of the mean distance of the reconstructed attractor was selected that produced linear changes in cross recurrence and a number of cross-recurrent points that was sufficiently low but not at floor level (Shockley, 2005). Those prescriptions guarantee, respectively, that results do not depend on the chosen radius and that floor effects are averted.

The cross recurrence quantification analysis measures MAXLINE and %REC are of particular relevance for studies of coordination because they are indices of λ and *Q*, respectively (e.g., Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005, 2006). MAXLINE, the longest sequence of

[2] Movement and breathing time series were represented as dynamical systems using attractor reconstruction (Abarbanel, 1996; Kennel, Brown, & Abarbanel, 1992; Takens, 1981). In attractor reconstruction, the goal is to "unfold" a scalar signal into the appropriate dynamical dimension. That was accomplished by identifying the time delay, τ, at which observations, X_i and $X_i + \tau$, were maximally independent (Takens, 1981). The value of τ was chosen using Abarbanel's (1996) prescription: the first minimum of the average mutual information function. False nearest neighbors (Kennel et al., 1992), a procedure used to examine whether neighboring data points in fewer dimensions separate, or are false, in higher dimensions, was then used to select the appropriate dynamical dimension. An optimal dimension is reached when the percentage of false nearest neighbors hits zero or becomes a vanishing fraction.

cross-recurrent points in a trial, reflects the amount of time the same trajectory can be maintained for movement and breathing in reconstructed space (Kudo et al., 2006; Shockley & Turvey, 2005). %REC, the percentage of the total number of points in a trial that are cross-recurrent, reflects shared activity between two embedded time series (Kudo et al., 2006; Shockley & Turvey, 2005). Note that an increase in MAXLINE implies an increase in %REC, indicating that differences in the magnitude of changes in each can be important. Despite that relation, MAXLINE was positively correlated with attractor stability, while %REC was inversely related to the magnitude of noise in interlimb coordination (Richardson et al., 2007). Stated differently, MAXLINE indexed the deterministic aspect of the HKB model, while %REC indexed the stochastic aspect.

Design

Unless otherwise noted, dependent measures from the second trial in each condition were analyzed with 2 (Pattern: inphase and antiphase) x 3 (Mass: 1 kg, 3 kg, and 5 kg) ANOVAs. Both Pattern and Mass were within-subjects factors.

Results

Frequency

Table 1 identifies preferred movement and breathing frequency and the variable error of movement and breathing frequency observed for baseline trials. One-way ANOVAs were performed on movement frequency and loaded breathing frequency over the Mass conditions (0 kg, 1 kg, 3 kg, 5 kg). The effect of Mass on movement frequency was significant, $F(3, 54) = 18.34$, $p < .001$, $\eta^2 = .51$. Movement frequency was similar in the 0 kg and 1 kg conditions,

$F(1, 18) = 0.10$, $p = .76$, $\eta^2 = .01$, but otherwise decreased with increasing weight: 1 kg vs. 3 kg, $F(1, 18) = 101.75$, $p < .001$, $\eta^2 = .85$; 3 kg vs. 5 kg, $F(1, 18) = 10.37$, $p < .01$, $\eta^2 = .37$. The effect of Mass on loaded breathing frequency was not significant, indicating that breathing frequency was similar with different masses attached to the leg. Loaded breathing frequency was collapsed across Mass and then compared to the resting breathing frequency in a one-way ANOVA. That comparison was not significant, indicating that resting and loaded breathing frequencies were similar. Across the board, the preferred movement frequencies were over twice as fast as the preferred breathing frequencies, indicating a frequency asymmetry.

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insert Table 1 about here.

The corresponding ANOVAs were performed on the variable error of movement frequency and loaded breathing frequency for baseline trials. The effect of Mass on the variable error of movement frequency was significant, $F(3, 54) = 7.07$, $p < .001$, $\eta^2 = .28$. The variable error of movement frequency was lower with than without additional weight, $F(1, 18) = 12.92$, $p < .01$, $\eta^2 = .42$, but was similar across the weight conditions: 1 kg vs. 3 kg, $F(1, 18) = 0.82$, $p = .38$, $\eta^2 = .04$; 1 kg vs. 5 kg, $F(1, 18) = 0.07$, $p = .80$, $\eta^2 = .004$; 3 kg vs. 5 kg, $F(1, 18) = 0.17$, $p = .69$, $\eta^2 = .01$. Movement frequency was less variable when ankle weights were attached to the leg. The effect of Mass on the variable error of loaded breathing frequency was not significant, indicating that the variability of

breathing frequency was similar with different masses attached to the leg. The variable error of loaded breathing frequency was collapsed across Mass and then compared to the variable error of resting breathing frequency in a one-way ANOVA. That ANOVA was significant, $F(1, 18) = 36.22$, $p < .001$, $\eta^2 = .67$. Although the mean breathing frequency did not change under a movement load, the variability of breathing frequency became higher.

Experimental manipulation checks. Analyses were performed to check whether movement and breathing frequency were at the prescribed 0.54 Hz and maintained a monofrequency relation during experimental trials. Movement frequency, breathing frequency, and their frequency ratio were collapsed across Pattern and Mass because those effects were not significant in ANOVAs. Movement frequency, $t(18) = 8.92$, $p < .001$, and breathing frequency, $t(18) = 8.84$, $p < .001$, were significantly different from a test value of 0.54 Hz in single sample t-tests. Movement (M = 0.535 Hz, SD = 0.002 Hz) and breathing frequencies (M = 0.536 Hz, SD = 0.002 Hz) were slightly slower than the prescribed pace. A t-test in which the frequency ratio was compared to 1.00 was not significant. Therefore, participants maintained a monofrequency relation between movement and breathing.

Relative Phase

The two main frequency asymmetry predictions were: as frequency asymmetry decreases (1) the breathing lead should decrease; and (2) the variability of relative phase performance should increase. Figure 8 depicts the constant error (top panel) and variable error (bottom panel) of relative phase

performance across Mass for inphase (solid line) and antiphase (dashed line) performance. Constant error was mostly negative, indicating that breathing led movement. The effect of Mass on constant error was significant, $F(2, 36) = 28.78$, $p < .001$, $\eta^2 = .62$. Contrasts between each subsequent mass were all significant: 1 kg vs. 3 kg, $F(1, 18) = 16.83$, $p < .01$, $\eta^2 = .48$; 3kg vs. 5 kg, $F(1, 18) = 15.58$, $p < .01$, $\eta^2 = .46$. Like predicted, as mass increased (i.e., $\Delta\omega$ decreased because the leg movement frequency became slower with the addition of mass), the degree to which breathing led movement decreased. The Pattern x Mass interaction was marginally significant, $F(2, 36) = 2.62$, $p = .087$, $\eta^2 = .13$. Simple effects of Pattern at each mass were performed on constant error. Only the simple effect at 1 kg was significant, $F(1, 18) = 4.26$, $p = .05$, $\eta^2 = .19$. Constant error was more negative (the breathing lead was larger) for inphase than antiphase performance at the largest $\Delta\omega$.

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insert Figure 8 about here.

The main effects of Pattern, $F(1, 18) = 6.94$, $p < .05$, $\eta^2 = .28$, and Mass, $F(2, 36) = 4.13$, $p < .05$, $\eta^2 = .19$, on variable error were significant. As expected, variability was higher for antiphase than for inphase performance. Contrasts were performed between each mass pair. Variable error was only different between the 1 kg and 5 kg masses, $F(1, 18) = 8.80$, $p < .01$, $\eta^2 = .33$. Consistent with predictions, the variability of relative phase performance was higher at the smallest than at the largest $\Delta\omega$.

Cross Recurrence Quantification Analysis

A time delay of 24 data points was used for attractor reconstruction, which approximated that estimated from the average mutual information function (*M* = 24.28 data points; *SD* = 0.10 data points). To guarantee sufficient unfolding and to be consistent across experiments in this dissertation, movement and breathing data were embedded in five dimensions. That embedding dimension approximated the estimate from false nearest neighbors analysis (*M* = 4.95 dimensions; *SD* = 0.37 dimensions) and was consistent with the dimensionality typical of biological data (Shockley, 2005). Figure 9 depicts the first three dimensions of sample reconstructed movement (top panels) and breathing (bottom panels) attractors for a single participant at the largest (1 kg; left panels) and smallest (5 kg; right panels) frequency asymmetries. The data were from performance in the inphase condition. Although the attractors maintained the same general character, the respective movement and breathing attractors were visibly less consistent at the largest frequency asymmetry than at the smallest frequency asymmetry.

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insert Figure 9 about here.

Figure 10 depicts cross recurrence plots created from the data in Figure 9 for the largest (1 kg; left panel) and smallest (5 kg; right panel) frequency asymmetries. For each plot, reconstructed movement and breathing pairs from the same trial were compared. Points were plotted at the coordinates *i*, *j* if the distance

between the movement and breathing data was within 21% of the mean distance of the reconstructed attractor. That is, the points in each plot represent cross-recurrences. An intuition for the meaning of %REC and MAXLINE can be gained through examination of the plots. %REC is the density of cross-recurrent points, regardless of the patterning of those points. Diagonal lines indicate common structure—shared movement and breathing trajectories. MAXLINE is the longest diagonal line in each plot. Both those characteristics were different between the plots in Figure 10. Values on both the cross recurrence measures were lower at the largest frequency asymmetry (%REC = 3.87; MAXLINE = 462) than the smallest frequency asymmetry (%REC = 5.20; MAXLINE = 569).

insert Figure 10 about here.

Cross recurrence quantification analysis was used to capture those changes analytically across participants. Figure 11 depicts %REC (top panel) and MAXLINE (bottom panel) across Mass for inphase (solid line) and antiphase (dashed line) performance. The Pattern x Mass interaction was significant for %REC and marginally significant for MAXLINE (see Table 2). The simple effects of Mass on both %REC and MAXLINE were significant at inphase but not at antiphase. At inphase, follow-up simple comparisons of 1 kg vs. 5 kg and 3 kg vs. 5 kg were significant on both measures. For inphase performance, there was a decrease in noise and an increase in attractor strength from the lighter masses (larger $\Delta\omega$) to the heavier, 5 kg mass (smallest $\Delta\omega$). For examples of the impact

of such changes on the form of attractors and cross recurrence plots see Figures 9 and 10, respectively. There were no differences on the cross recurrence measures for antiphase performance at the different frequency asymmetries. The simple effect of Pattern at 5 kg was also significant for %REC and MAXLINE. Values on both measures were higher for inphase than antiphase performance at 5 kg. Stochastic and deterministic properties of performance differed for inphase and antiphase but only in the heaviest mass (smallest $\Delta\omega$) condition.

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insert Figure 11 and Table 2 about here.

Discussion

In Experiment 1, there was a breathing lead that increased with larger $\Delta\omega$ between movement and breathing. That result was consistent with the predictions derived from the HKB model (Haken et al., 1985) and, therefore, the theoretical interpretation in the interlimb coordination literature (e.g., Amazeen et al., 1996, 1998a; Rosenblum & Turvey, 1988; Schmidt et al., 1993; Sternad et al., 1992, 1996; Turvey et al., 1986). Lead-lag relations have been lawfully related to a ratio of the frequency characteristics of each component (Rosenblum & Turvey, 1988; Turvey et al., 1986, 1988). The same is probably true for motor-respiratory coordination, although an accurate breathing frequency estimate is elusive at present. As a collective measure, that ratio indexes properties of a higher-level coordinative structure (Bernstein, 1967). As such, properties of that structure are different from those of the very many underlying degrees of freedom associated

with coordination. Therefore, motor-respiratory coordination cannot be understood by reducing its description down to lower-level components.

In most wrist-pendulum studies (e.g., Amazeen et al., 1996, 1998a; Schmidt et al., 1993; Sternad et al., 1992, 1996; Treffner & Turvey, 1995; Turvey et al., 1986), the variability of coordination tends to increase with larger relative phase deviations. In the current study, relative phase variability decreased with larger relative phase deviations. Although that pattern of results departs from more elementary coordination dynamics, it has been observed previously. For example, the coordination of differently oriented pendulums (one up, the other down) displayed lower constant error at positive $\Delta\omega$ but similar variable error compared to that of identically oriented pendulums (Amazeen et al., 1998b; see also Mulvey, Amazeen, & Riley, 2005). In a study on handedness and lateralized attention, the constant error of coordination increased when participants attended to the dominant hand but variable error decreased (Amazeen, Amazeen, Treffner, & Turvey, 1997). Those results, which were a function of asymmetries in orientation and attention, suggest the relation between constant error and variable error in the current study might also be a function of asymmetry.

On the basis that the natural state of motor-respiratory coordination is asymmetric, relative phase variability was predicted to decrease with larger relative phase deviations. Across exercises (Amazeen et al., 2001; Garlando et al., 1985; Mahler, Hunter, et al., 1991), movement and breathing are always asymmetric. The current result rephrased: relative phase variability decreased the closer movement and breathing were to their naturally asymmetric state.

Manipulations of orientation and attention might produce an inherently asymmetric coordinative system (Amazeen et al., 1997, 1998b; Mulvey et al., 2005) in which the same hypothesis would apply. A reason that the results of most wrist-pendulum studies might differ is that the coordinative components are inherently symmetric (Haken et al., 1985). That is, aside from a small but systematic asymmetry associated with handedness (Treffner & Turvey, 1995, 1996), the hands holding the pendulums are symmetric oscillators.

A detailed analysis of more naturally detuned systems such as coordinated arm and leg movement (Jeka & Kelso, 1995; Kelso & Jeka, 1992) could lend further support to the above interpretation for motor-respiratory coordination. Motor-respiratory coordination and coordinated arm and leg movement are fundamentally similar in the magnitude of the frequency asymmetry between components. Despite the fact that one involves coordination between bodily subsystems and the other, coordination within the motor subsystem, the effects of frequency asymmetry on coordination could be similar. The implication is that coordinated arm and leg movement may be more similar to motor-respiratory coordination than to other, more symmetric forms of interlimb coordination. Ankle weights, like those in the current study, could be used to systematically examine different frequency asymmetries in coordinated arm and leg movement. To my knowledge, that manipulation has yet to be performed.

The marginally larger breathing lead for inphase than antiphase performance at large $\Delta\omega$ also suggests that frequency asymmetry was an advantage in motor-respiratory coordination. Stated differently, more stable

performance better approximated the naturally detuned state at large $\Delta\omega$. No such interaction was observed for relative phase variability although, consistent with predictions of the HKB model (Haken et al., 1985; Kelso et al., 1990), the variability of performance was significantly greater for antiphase than inphase. The cross recurrence results did not parallel the relative phase variability results, and were not wholly consistent with predictions because, in particular, %REC and MAXLINE were constant over $\Delta\omega$ in the antiphase condition. Differences between inphase and antiphase performance on %REC and MAXLINE were most evident, and in the expected direction, at the smallest $\Delta\omega$. In that condition, inphase performance was lower in noise and higher in attractor strength than antiphase performance. Thus, differences in those cross recurrence measures became most evident furthest from the natural motor-respiratory asymmetry.

Experiment 2: Frequency Asymmetry and Oscillation Frequency

In Experiment 1, attraction to inphase and antiphase was exhibited but the observed relative phases were lower than the expected relative phases (i.e., less than 0° relative phase or less than 180° relative phase, respectively) due to physical differences between movement and breathing. The oscillator of slower natural frequency, breathing, led the oscillator of faster natural frequency, leg movement. That breathing lead varied with the relative phase pattern performed. Oscillation frequency can also magnify the extent to which one oscillator leads another and increase the variability of performance (Amazeen et al., 1996), particularly at larger $\Delta\omega$ (when the component frequencies are quite different; Schmidt et al., 1993; Sternad et al., 1992). Given oscillation frequency has been identified as a control parameter in coordination research (e.g., Kelso, 1984), those results are noteworthy. They suggest that transitions in performance may begin through initially small shifts away from relative phase attractors. Moreover, in systems with larger frequency asymmetry that are tuned further from those stable relative phase attractors, transitions might be more likely to occur (Kelso & Jeka, 1992). Experiment 2 was designed to explore the interaction of oscillation frequency with frequency asymmetry in motor-respiratory coordination.

Participants were instructed to perform inphase at different oscillation frequencies with ankle weights of various mass. Inphase was chosen because the magnitude of changes that resulted from different frequency asymmetries was larger for inphase than for antiphase performance in Experiment 1. The result of Experiment 1 in which relative phase stability was greatest at the largest

frequency asymmetry suggests that we cannot expect the same pattern of results from interlimb coordination in motor-respiratory coordination. From the HKB model (Equation 1), one would expect more stable performance to be less affected by oscillation frequency (e.g., Kelso, 1984). Predictions were, therefore, based on expectations for more versus less stable performance at various frequency asymmetries in the HKB model and previous motor-respiratory coordination results (Experiment 1; Temprado et al., 2002).

Figure 12 depicts constant error (top panel) and variable error (bottom panel) predictions over various $\Delta\omega$ for slow (circles) and fast (triangles) frequencies. Because only negative $\Delta\omega$ were used, predicted shifts in attractor location are in the negative direction. Breathing was expected to lead movement (see Experiment 1; Temprado et al., 2002). As $\Delta\omega$ increases, those shifts become more negative. With a reduction in the mass attached to the ankle (larger $\Delta\omega$), breathing was expected to further lead movement and the variability of performance was expected to decrease (a replication of Experiment 1). For a given $\Delta\omega$, performance at the fast frequency should shift away from the natural motor-respiratory asymmetry (i.e., toward a constant error of 0°) and increase the variability of performance compared to performance at the slow frequency. Both of those effects were anticipated to be larger when the natural frequencies of movement and breathing were more similar (smaller $\Delta\omega$).

insert Figure 12 about here.

Replicating the results for inphase performance in Experiment 1, %REC and MAXLINE were expected to decrease from the smallest to the largest Δω. That frequency asymmetry would both increase noise and decrease attractor strength is consistent with hypotheses (Fuchs & Kelso, 1994; Riley et al., 2001) and results in interlimb coordination (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005). Interlimb coordination results also suggest that with variation in oscillation frequency, changes in attractor strength should be more pronounced than changes in noise (Richardson et al., 2007). Consistent with those results, the decrease in MAXLINE from a slower to faster oscillation frequency was expected to be larger in magnitude than the decrease in %REC. That is, both Δω and oscillation frequency were expected to influence attractor strength and noise.

Method

Participants

Thirteen participants (11 men, 2 women; 18–27 years old) received credit toward their introductory psychology course in exchange for their participation. Exclusion criteria were the same as in Experiment 1. All participants were treated in accordance with the ethical principles of the American Psychological Association.

Apparatus

Task characteristics and data collection were the same as in Experiment 1.

Procedure

The baseline procedure was the same as in Experiment 1. For familiarization and experimental trials, unlike the other experiments in this dissertation, participants only performed the inphase pattern. There were two familiarization trials with a metronome at a comfortable frequency, 0.54 Hz, and a fast frequency, 0.78 Hz (order counterbalanced). Familiarization trials were used because participants had difficulty synchronizing with the 0.78 Hz frequency without practice. The fast 0.78 Hz frequency was 20% lower than the average maximum frequency pilot participants could maintain for a 60 s period with a 5 kg ankle weight. Two 60 s experimental trials followed in which inphase was performed twice at each frequency (order counterbalanced) with each mass (order randomized): 1 kg (largest $\Delta\omega$), 3 kg, and 5 kg (smallest $\Delta\omega$). Duplicate trials were collected to ensure there was at least one analyzable trial per condition. A minimum 30 s rest was provided between each trial to minimize fatigue. More rest was provided upon request.

Calculations, Dependent Measures, and Design

Calculations and dependent measures were the same as in Experiment 1. Unless otherwise noted, dependent measures from the second trial in each condition were analyzed with 2 (Metronome Frequency: 0.54 Hz and 0.78 Hz) x 3 (Mass: 1 kg, 3 kg, and 5 kg) ANOVAs. Both Metronome Frequency and Mass were within-subjects factors.

Results

Frequency

Table 3 identifies preferred movement and breathing frequency and the variable error of movement and breathing frequency observed for baseline trials. All of the baseline frequency results mirrored those of Experiment 1, except that the change in leg movement frequency, although in the expected direction, was somewhat reduced. A one-way ANOVA was performed on movement frequency and loaded breathing frequency over the Mass conditions (0 kg, 1 kg, 3 kg, 5 kg). The effect of Mass on movement frequency was significant, $F(3, 36) = 5.03$, $p < .01$, $\eta^2 = .30$. Movement frequency was similar at 0 kg and 1 kg, $F(1, 12) = 0.02$, $p = .91$, $\eta^2 = .001$, but otherwise decreased with increasing mass: 1 kg vs. 3 kg, $F(1, 12) = 9.97$, $p < .01$, $\eta^2 = .45$; 3 kg vs. 5 kg, $F(1, 12) = 16.48$, $p < .01$, $\eta^2 = .58$. The effect of Mass on loaded breathing frequency was not significant, indicating that breathing frequency was similar with different masses attached to the leg. Loaded breathing frequency was collapsed across Mass and compared to the resting breathing frequency in a one-way ANOVA. That comparison was not significant, indicating the resting and loaded breathing frequencies were statistically similar. Movement frequencies were over twice as fast as the breathing frequencies, which reflects their natural asymmetry.

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insert Table 3 about here.

The corresponding ANOVAs were performed on the variable error of movement frequency and loaded breathing frequency for baseline trials. The effect of Mass on the variable error of movement frequency was significant, $F(3, 36) = 3.55$, $p < .05$, $\eta^2 = .23$. The variable error of movement frequency was lower with than without additional weight, $F(1, 12) = 7.96$, $p < .05$, $\eta^2 = .40$, but was similar across the weight conditions: 1kg vs. 3 kg, $F(1, 12) = 3.78$, $p = .08$, $\eta^2 = .24$; 1 kg vs. 5 kg, $F(1, 12) = 0.00$, $p = .98$, $\eta^2 = .00$; 3 kg vs. 5 kg, $F(1, 12) = 1.19$, $p = .30$, $\eta^2 = .09$. Movement frequency was less variable with than without the ankle weights. The effect of Mass on the variable error of loaded breathing frequency was not significant, indicating that the variability of breathing frequency was similar with different masses attached to the leg. The variable error of loaded breathing frequency was collapsed across Mass and compared to the variable error of resting breathing frequency in a one-way ANOVA. That comparison was significant, $F(1, 12) = 4.84$, $p < .05$, $\eta^2 = .29$. While the mean breathing frequency did not change significantly under a movement load, the variability of breathing frequency increased.

Experimental manipulation checks. Analyses were performed to determine if movement and breathing frequency were at 0.54 Hz during slow frequency trials and 0.78 Hz during fast frequency trials, and if a monofrequency relation was maintained during all experimental trials. Main effects of Metronome Frequency on movement frequency, $F(1, 12) = 391{,}141.20$, $p < .001$, $\eta^2 = 1.00$, and breathing frequency, $F(1, 12) = 146{,}550.50$, $p < .001$, $\eta^2 = 1.00$, were significant in an ANOVA. Movement and breathing frequency were lower

in the 0.54 Hz condition (movement: M = 0.533 Hz, SD = 0.001 Hz; breathing: M = 0.534 Hz, SD = 0.001 Hz) than the 0.78 Hz condition (movement: M = 0.769 Hz, SD = 0.001 Hz; breathing: M = 0.770 Hz, SD = 0.002 Hz). Those measures were collapsed across Mass for further analyses because no effects involving Mass were significant. Comparisons of movement frequency in the slow frequency condition to 0.54 Hz, $t(12) = 18.31$, $p < .001$, and in the fast frequency condition to 0.78 Hz, $t(12) = 21.41$, $p < .001$, were significant in t-tests. The same comparisons were significant for breathing frequency: 0.54 Hz, $t(12) = 29.38$, $p < .001$; 0.78 Hz, $t(12) = 15.96$, $p < .001$. Movement and breathing frequencies were slightly but significantly slower than the prescribed paces. Those lagging frequencies were not a problem because the main effects of Metronome Frequency were also significant. Those main effects indicate that the slow versus fast frequency manipulation was still effective. The frequency ratio was collapsed across Mass and Metronome Frequency because no effects involving those factors were significant. A t-test in which the frequency ratio was compared to 1.00 was not significant, indicating that participants maintained the monofrequency requirement during experimental trials.

Relative Phase

Figure 13 depicts the constant error (top panel) and variable error (bottom panel) of inphase performance across Mass for performance at 0.54 Hz (circles) and 0.78 Hz (triangles). Consistent with Experiment 1, constant error was negative, indicating that breathing led movement. The Mass x Metronome Frequency interaction was significant for constant error and variable error (see

Table 4). For constant error, the simple effects of Mass were significant but opposite in direction at 0.54 Hz and 0.78 Hz. Contrasts indicated those effects were between the largest Δω (1 kg) and smaller Δω (3 kg and 5 kg). At 0.54 Hz, the effect was consistent with predictions: the breathing lead decreased from the largest to smaller frequency asymmetries. At 0.78 Hz, the effect was opposite predictions: the breathing lead increased from the largest to smaller frequency asymmetries. For variable error, the simple effect of Mass was not significant at 0.54 Hz but was significant at 0.78 Hz. Contrasts indicated that the significant effect at 0.78 Hz was between larger Δω (1 kg and 3 kg) and the smallest Δω (5 kg). Relative phase variability was similar for different frequency asymmetries at 0.54 Hz but increased from the larger to smallest frequency asymmetry at 0.78 Hz. Those variability results were not consistent with predictions.

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insert Figure 13 and Table 4 about here.

Cross Recurrence Quantification Analysis

Time delays of 24 data points and 17 data points were used for attractor reconstruction at 0.54 Hz and 0.78 Hz, respectively. As time delays are directly related to cycle length, two different delays were necessary. Those time delays approximated estimates from the average mutual information function (0.54 Hz: M = 24.44 data points, SD = 0.20 data points; 0.78 Hz: M = 17.05 data points, SD = 0.06 data points). To guarantee sufficient unfolding, movement and

breathing data were embedded in five dimensions. That dimensionality approximated the estimates from false nearest neighbors analysis (0.54 Hz: *M* = 4.92 dimensions, *SD* = 0.37 dimensions; 0.78 Hz: *M* = 4.95 dimensions, *SD* = 0.64 dimensions). Data were considered cross-recurrent if the distance between points was within 21% of the mean distance of the reconstructed attractor.

Figure 14 depicts %REC (top panel) and MAXLINE (bottom panel) across Mass for performance at 0.54 Hz (circles) and 0.78 Hz (triangles). The Mass x Metronome Frequency interaction was significant for %REC (see Table 5). For %REC, the simple effects of Mass were significant at both 0.54 Hz and 0.78 Hz. The effect at 0.54 Hz was between the largest Δω (1 kg) and smaller Δω (3 kg and 5 kg), and at 0.78 Hz, there were differences between all Δω (1 kg, 3 kg, and 5 kg). For those effects, %REC increased with mass at 0.54 Hz, and decreased with mass at 0.78 Hz. From the larger to smaller frequency asymmetries, noise between movement and breathing decreased at 0.54 Hz and increased at 0.78 Hz. Only the effect at 0.54 Hz was consistent with predictions, although the %REC results were consistent with what would be expected from the constant error results (i.e., the same pattern of results in the top panels of Figures 13 and 14).

insert Figure 14 and Table 5 about here.

The main effect of Mass on MAXLINE was significant, although that effect was subsumed by a marginally significant Mass x Metronome Frequency interaction (see Table 5). Only the simple effect of Mass at 0.78 Hz was significant for MAXLINE. That effect was between the larger $\Delta\omega$ (1 kg and 3 kg) and the smallest $\Delta\omega$ (5 kg). For those significant effects, MAXLINE decreased with increased mass. From the larger to smallest $\Delta\omega$, attractor strength decreased. Together, the %REC and MAXLINE results suggest that frequency asymmetry influenced only noise at the comfortable frequency, and both noise and attractor strength at the fast frequency. For examples of the impact of such changes on the form of attractors and cross recurrence plots see Figures 9 and 10, respectively.

Discussion

The influence of $\Delta\omega$ on relative phase performance was different at slower and faster oscillation frequencies. I will first discuss the results at the slower, comfortable oscillation frequency. Consistent with predictions of the HKB model (see Equation 1) and the results of Experiment 1, the breathing lead increased at the comfortable frequency with a larger $\Delta\omega$ between movement and breathing. Participants were better able to perform a perfect inphase pattern when components involved in the coordination were more similar. That result reflects observations within the motor subsystem of the body (Rosenblum & Turvey, 1988; Turvey et al., 1986) in coordination between bodily subsystems. The decrease in relative phase variability with the increase in $\Delta\omega$ observed in Experiment 1 was not replicated here. That difference could be related to carry-over effects from the faster oscillation frequency condition (discussed below)

and/or the smaller magnitude of change in movement frequency with ankle weights observed in the current experiment.

Similar to the results of Experiment 1, at the comfortable frequency, the attractor dynamic was less noisy at smaller than larger $\Delta\omega$. That result is consistent with observations in interlimb coordination (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005). The concomitant increase in attractor strength observed in Experiment 1 was not replicated here. Given those different results, it is not entirely clear whether the increase in noise and reduction in attractor strength observed in wrist-pendulum studies with increased $\Delta\omega$ (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005) also applies to motor-respiratory coordination. To clarify, motor-respiratory coordination studies should be performed with different types of movements to eliminate the possibility that the results observed in this study were a function of the protocol. For example, resistance applied to the wheel rim on a bicycle or wheelchair would decrease the natural frequency of the movements in those tasks.

At the fast oscillation frequency, there were increases in the breathing lead and relative phase variability from larger to smaller $\Delta\omega$. That accuracy result was opposite the direction of the accuracy results in Experiment 1 and differed from predictions of the HKB model (Kelso et al., 1990) and observations from wrist-pendulum studies (e.g., Rosenblum & Turvey, 1988; Turvey et al., 1986). It is possible that spring-like properties (Turvey, 1990; Turvey et al., 1988) of movement changed from the comfortable to the fast frequency. If the stiffness of leg movement decreased at the faster frequency, then the breathing lead would

increase. That hypothesis could be explored in future research through the use of Hooke's portraits (Mottet & Bootsma, 1999), a method of distinguishing between tight and loose springs. A carry-over effect from the faster to slower frequency conditions might have also reduced the influence of the frequency asymmetry on relative phase accuracy. Frequency was manipulated within mass blocks, therefore, faster frequency performance in one mass condition could influence slower frequency performance in another mass condition. That influence could, in turn, explain how $\Delta\omega$ could affect relative phase variability at the comfortable frequency in Experiment 1 but not in this experiment.

As indicated by the cross recurrence results, performance was generally lower in noise and higher in attractor strength at the comfortable frequency than at the fast frequency. That result was consistent with the results of Experiment 1. Differences in the magnitude of effects on attractor strength and noise, as observed in wrist-pendulum work (Richardson et al., 2007), were not observed here. Not too much should be made of those slight differences, though, because additional work needs to be done to clarify exactly what constitutes a meaningful difference in magnitude, perhaps focusing on differences in effect size. There were, however, interactions in which the effect of $\Delta\omega$ on %REC and MAXLINE differed for performance at the comfortable and fast frequencies. For performance at the fast frequency, the increase in noise and decrease in attractor strength was amplified at smaller $\Delta\omega$. That result suggests, consistent with the results of Experiment 1, that more symmetric performance may be more difficult in motor-respiratory coordination because it is a less natural tuning.

Experiment 3: More Complex Dynamics

A substantial frequency asymmetry was observed between movement and breathing in Experiments 1 and 2. Frequency asymmetry has been hypothesized to be at the core of some more complex relative phase dynamics (Kelso & Jeka, 1992). That connection was originally established in the field of behavioral physiology (e.g., von Holst, 1973). Early observations (between 1932 and 1962; not translated into English until 1973) were made by a pioneering German behavioral physiologist, Erich von Holst. The now classic example, first detailed by von Holst, is the coordination of rhythmically moving fish fins. With the connection between the brain and spine cut, larger fins (e.g., tail fins) oscillated independent of and at a slower frequency than smaller fins (e.g., pectoral fins). In fish that had not undergone surgery, von Holst identified two competing tendencies in the coordination of fins. There was a tendency for each fin to maintain its characteristic frequency, the maintenance tendency, coupled with a tendency for each fin to impose its characteristic frequency on the other fin, the magnet effect. von Holst's interpretation with regard to those competing tendencies is particularly relevant to the study of more complex dynamics in motor-respiratory coordination.

If the maintenance tendency dominated, then von Holst (1973) postulated that a particular category of coordination, relative coordination, would be exhibited. In von Holst's observations, fish fins typically moved neither independently nor in an entirely fixed relation. That less-rigid, more flexible form of coordination (Kelso & Jeka, 1992; Turvey, 1990) was manifested in a variety

of ways. A brief exposition of a few of those ways, although not analyzed for in the current experiment, is of interest to see the variety. In the superimposition effect, which bears an uncanny resemblance to sound wave interactions (e.g., Plack, 2005), the net amplitude of fins coordinated inphase was the sum of the individual fin amplitudes in isolation. When coordinated antiphase, the net amplitude was lower than either of the individual fin amplitudes in isolation. Phase resetting was also observed in which the phase angle of one fin would suddenly change, typically matching the phase angle of the other fin. Moreover, periodicities in frequency and amplitude were observed, consistent with the kinds of behavior exhibited in systems like the Lorenz attractor under certain parameter settings prior to the onset of chaos (May, 1976).

Examples of relative coordination have also been observed in human behavior. Following seminal research on symmetric oscillators (Kelso, 1984), Kelso and Jeka (1992) instructed participants to coordinate the arms and legs at increasing frequencies of oscillation. At critical, faster oscillation frequencies sudden, spontaneous transitions (phase transitions) from stable relative phase patterns toward phase wrapping and intermittency were observed. In phase wrapping, all relative phases are visited in a periodic fashion. Intermittency, periods of phase attraction that occur along with periods of phase wrapping, is evidence of a ghost attractor (Kelso & Ding, 1993; Mitra, Amazeen, & Turvey, 1997; Strogatz, 1994). Both categories of complex relative phase dynamics are distinguishing features of self-organized systems (Haken, 1996). Intermittency, in

particular, is empirical evidence of the synchronization/desynchronization that von Holst (1973) deemed relative coordination.

Transitions to phase wrapping and intermittent behavior, although inconsistent with predictions of the original HKB model (Haken et al., 1985), are predicted from the later asymmetric extension of the model (Kelso et al., 1990). When the magnitude of the frequency asymmetry term, $\Delta\omega$, is very large, stable relative phase solutions can be eliminated, leaving only running or phase wrapping solutions (Fuchs, Jirsa, Haken, & Kelso, 1995; Kelso et al., 1990; Kelso & Ding, 1993; Kelso & Jeka, 1992; Mitra et al., 1997). Such transitions are referred to as saddle-node bifurcations in which the collision of unstable and stable states is followed by their annihilation (Mitra et al., 1997; Strogatz, 1994). Intermittency results from the persistence of a saddle-node ghost attractor that attracts and repels (Mitra et al., 1997), and is captured in the motion equation function. In the temporal evolution of phase wrapping, behavior traverses more slowly through relative phases that correspond to derivatives closer to zero (i.e., lower velocities; Kelso et al., 1990; Kelso & Ding, 1993; Kelso & Jeka, 1992).

In Experiment 3, the phase transition paradigm (Kelso, 1984; Kelso & Jeka, 1992) was employed in which participants were instructed to perform the inphase and antiphase patterns during motor-respiratory coordination at increasing frequencies of oscillation. As mentioned previously, the magnitude of the frequency asymmetry between components makes motor-respiratory coordination fundamentally similar to coordination between the arms and legs. The hypothesis explored here is that the dynamics in motor-respiratory coordination and

coordination between the arms and legs might be more similar than coordination between the arms and legs is to more symmetric forms of interlimb coordination. Therefore, following from the asymmetric extension of the HKB model (Equation 1), sudden transitions from antiphase and inphase toward phase wrapping and intermittency were predicted because of the substantial frequency asymmetry between movement and breathing.

Method

Participants

Thirteen participants (10 men, 3 women; 18–23 years old) received credit toward their introductory psychology course in exchange for their participation. Exclusion criteria were the same as in Experiment 1. All participants were treated in accordance with the ethical principles of the American Psychological Association.

Apparatus

Task characteristics and data collection were the same as in Experiment 1, except that ankle weights were not attached to the leg.

Procedure

The baseline procedure was the same as in Experiment 1 with the following exceptions: (1) there were no baseline conditions with ankle weights; and (2) a coupled baseline trial was performed following uncoupled baseline trials like those performed in Experiment 1. The coupled trial was designed to get an estimate of frequency preferences when participants were instructed to move and breathe at the same speed. It allowed for the assessment of how much participants

exceeded that frequency preference in the phase transition paradigm. Each participant swung the right leg forward and backward in the sagittal plane and breathed once per movement cycle. Participants were allowed to select any relative phase pattern between movement and breathing. The coupled baseline trial was 60 s in length.

For experimental trials, participants were instructed to perform inphase or antiphase (order counterbalanced). They were allowed one 60 s trial to practice the instructed pattern at a slow metronome frequency (0.3 Hz). They then performed two 120 s trials, beginning each trial with the instructed pattern. The metronome frequency increased from 0.3 Hz in eight 0.15 Hz plateaus. The duration of each plateau was 15 s. Participants were told both to complete one full movement cycle and one full breathing cycle per metronome tone and to maintain the starting pattern but, if a different pattern felt more comfortable, not to resist switching (e.g., Kelso, 1984; Kelso & Jeka, 1992; Kelso, Scholz, & Schöner, 1986; Kelso et al., 1987; Scholz & Kelso, 1989; Schöner et al., 1986). A 1 min rest between each trial was required to minimize fatigue. More rest was provided upon request. Participants were instructed to stop if they felt at risk of hyperventilation. Two participants stopped prior to the completion of all frequency plateaus on at least one trial.

Calculations and Dependent Measures

Calculations and dependent measures were the same as in Experiment 1, except that certain measures were calculated plateau-by-plateau to examine their evolution over changes in oscillation frequency. The 0.3 Hz plateau was excluded

from the analysis to account for a settling-in period with the metronome. To avoid anomalies associated with a switch from one frequency to the next, the timestamp at the second movement or breathing maximum (whichever came first) after a frequency change was considered the start of each plateau. The second maximum was used to allow some time for the frequency change to take effect. The timestamp at the next frequency change was considered the end of each plateau. A timestamp was used because the end of a plateau need not correspond to a movement or breathing maximum. Because each plateau was 15 s in length and the slowest frequency plateau analyzed was 0.45 Hz, the number of data points per plateau (minimum ≈ 528 data points) was sufficient for analysis.

Results

Frequency

Table 6 identifies mean movement and breathing frequency and the variable error of movement and breathing frequency for baseline trials. A one-way ANOVA in which the uncoupled and coupled movement frequencies were compared was significant, $F(1, 12) = 8.52$, $p < .05$, $\eta^2 = .42$. Movement frequency was faster in the uncoupled condition than the coupled condition. A one-way ANOVA in which the three breathing frequencies were compared (resting, loaded, and coupled) was also significant, $F(2, 24) = 39.42$, $p < .001$, $\eta^2 = .77$. As in Experiments 1 and 2, the resting and loaded breathing frequencies were not statistically different, $F(1, 12) = 0.26$, $p = .62$, $\eta^2 = .02$. Breathing frequencies were slower in the uncoupled conditions than the coupled condition: resting vs. coupled, $F(1, 12) = 48.95$, $p < .001$, $\eta^2 = .80$; loaded vs. coupled, $F(1, 12) =$

37.84, $p < .001$, $\eta^2 = .76$. Uncoupled movement frequency was also faster than the uncoupled breathing frequencies, reflecting their frequency asymmetry. When participants were instructed to move and breathe at the same frequency (the coupled condition), an intermediate mean frequency of 0.54 Hz was performed.

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insert Table 6 about here.

The corresponding ANOVAs were performed on the variable error of movement frequency and breathing frequency for baseline trials. Variable error was not statistically different for the uncoupled and coupled movement frequencies, $F(1, 12) = 2.66$, $p = .13$, $\eta^2 = .18$. Movement frequency was faster but not more variable in the uncoupled condition than the coupled condition. The one-way ANOVA comparing the variable error of the three breathing frequencies (resting, loaded, and coupled) was marginally significant, $F(2, 24) = 3.30$, $p = .054$, $\eta^2 = .22$. The variable error of breathing frequency was marginally higher in the loaded condition than the other two conditions: loaded vs. resting, $F(1, 12) = 3.39$, $p = .09$, $\eta^2 = .22$; loaded vs. coupled, $F(1, 12) = 4.13$, $p = .07$, $\eta^2 = .26$. Consistent with Experiments 1 and 2, the mean breathing frequency did not change with a movement load but the variability of breathing frequency increased marginally. Breathing frequency was also marginally less variable when participants were instructed to move and breathe at the same frequency (coupled breathing) than without the monofrequency requirement (loaded breathing).

Analyses were performed to determine if movement and breathing frequency were at the prescribed frequency for each plateau. Figure 15 depicts movement frequency (top panels) and breathing frequency (bottom panels) for inphase (left panels) and antiphase (right panels) performance. Prescribed frequencies are depicted as circles and mean performed frequencies as solid lines. Statistical variation is displayed in 95% confidence intervals (gray areas). If the prescribed frequencies lay within the confidence intervals, then the performed frequencies statistically approximated the prescribed frequencies. Lagging behind the faster prescribed frequencies was evident as there was a bend in the right side of each graph. The performed frequencies at the 1.05 Hz, 1.20 Hz, and 1.35 Hz plateaus were compared to the prescribed frequencies for those plateaus in a series of t-tests (presented in Table 7). All were significant, indicating that the performed frequencies were statistically slower than the fast prescribed frequencies. The different degrees of freedom reflect the fact that certain participants could not complete all of the frequency plateaus. Those lagging frequencies might have prevented some transitions in performance but should not be considered a major problem. Consistent with the monofrequency requirement, similar movement and breathing frequencies were displayed within each relative phase condition at each separate plateau.

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insert Figure 15 and Table 7 about here.

Differences in the ability to maintain the faster prescribed frequencies were apparent for inphase and antiphase performance (see Figure 15). Movement frequency and breathing frequency were analyzed in separate 2 (Pattern: inphase and antiphase) x 7 (Frequency Plateau (Hz): 0.45, 0.60, 0.75, 0.90, 1.05, 1.20, and 1.35) within-subjects ANOVAs. The main effects of Pattern and Frequency Plateau on movement frequency and breathing frequency were significant (see Table 8). Movement and breathing frequencies were generally faster for inphase than antiphase performance because participants were better able to maintain the prescribed frequencies. Contrasts between each subsequent frequency plateau were all significant, indicating that the performed frequency always increased from one plateau to the next. The Pattern x Frequency Plateau interactions were also significant for movement frequency and breathing frequency. As indicated by the marginally significant interaction contrast, the increase in movement frequency and breathing frequency from the 1.20 Hz to 1.35 Hz plateaus was larger when participants performed inphase than when they performed antiphase.

insert Table 8 about here.

Relative Phase

During familiarization trials, the constant error of relative phase performance was mostly negative, which indicates that breathing generally led movement (inphase: M = -37.87°, SD = 20.82°; antiphase: M = -32.87°, SD = 24.10°). One-way ANOVAs were performed over Pattern on the constant

error and variable error of relative phase performance. The main effect of Pattern was not significant on constant error, $F(1, 12) = 0.84$, $p = .38$, $\eta^2 = .07$, but was significant on variable error, $F(1, 12) = 11.67$, $p < .01$, $\eta^2 = .49$. The accuracy of inphase and antiphase performance did not differ during familiarization trials, but the variability of inphase performance ($M = 27.23°$; $SD = 3.99°$) was lower than antiphase performance ($M = 33.50°$; $SD = 7.20°$), as expected from predictions of the HKB model (Haken et al., 1985; Kelso et al., 1990).

For experimental trials, participants began by performing inphase or antiphase at a slow frequency and then gradually increased that frequency. Transitions were flagged on a participant-by-participant basis by identifying the timestamp at which variable error exceeded twice that observed during familiarization trials. All the transitions were toward phase wrapping and intermittency. To visualize, continuous relative phase plots were produced over the frequency plateaus for representative transitions in the inphase (top panels) and antiphase (bottom panels) conditions (see Figure 16). Performance began around inphase (0°) or antiphase (180°) at slower frequency plateaus and transitioned into phase wrapping (diagonal stripes across the plots) and/or intermittency (areas of flattening within those diagonal stripes) at faster frequency plateaus. A few examples of phase wrapping and intermittency are labeled in the plots. Consistent with the higher stability of inphase performance, fewer transitions were observed from inphase (46.15% of trials) than from antiphase (69.23% of trials) toward phase wrapping and/or intermittency. The frequency plateau at which those transitions occurred varied across participants (from

inphase: *M* = 1.15 Hz, *Range* = 0.90 Hz to 1.35 Hz; from antiphase: *M* = 1.08 Hz, *Range* = 0.90 Hz to 1.35 Hz). A meaningful statistical comparison of those transition points could not be performed due to an unequal number of transitions by Pattern. Therefore, it was not clear if participants could maintain inphase at a faster frequency than antiphase. Given the complex dynamics exhibited in continuous relative phase performance, an analysis of mean constant error and variable error is meaningless because there was no central tendency.

insert Figure 16 about here.

Cross Recurrence Quantification Analysis

Cross recurrence quantification analysis was used to examine the consequences of those transitions for the attractor dynamic. Only those trials during which transitions occurred (see percentages above) were included in the analysis. Attractor reconstruction parameters are identified in Table 9. The time delays used approximated those observed from the average mutual information function. Note how the time delays decreased as the prescribed frequency increased. That inverse relation was a function of differences in cycle length at lower and higher frequencies. As in Experiments 1 and 2, five dimensions were used for embedding. That dimensionality was high for the lower frequency data is not of great consequence to the reconstruction (some introduction of higher-dimensional noise; Shockley, 2005). To avoid introducing confounds in the estimation of cross recurrence measures, maintenance of a constant

dimensionality is more imperative (Shockley, 2005). Points were cross-recurrent if they were within 21% of the mean distance of the reconstructed attractor.

insert Table 9 about here.

Because the plateau at which transitions occurred varied from participant to participant, the cross recurrence data needed to be aligned so that those transitions corresponded. Figure 17 depicts the aligned %REC (top panel) and MAXLINE (bottom panel) data for inphase (solid line) and antiphase (dashed line) performance. Due to an unequal number of transitions by Pattern, separate within-subjects ANOVAs were run for the inphase and antiphase conditions. To include as many participants as possible, the analysis was restricted to plateaus 1–4. Those plateaus were before the transition (plateaus 1 and 2), at the transition (plateau 3), and after the transition (plateau 4). Due to stoppage before plateau 4, two participants were excluded from the inphase analysis and one participant was excluded from the antiphase analysis. The results of the ANOVAs, identified in Table 10, will be discussed next.

insert Figure 17 and Table 10 about here.

For inphase performance, the main effect of Frequency Plateau was only significant on %REC. The number of participants (n = 4) in the inphase analysis was small because there were so few transitions and participants were excluded

from the analysis. For antiphase performance, both the main effects of Frequency Plateau on %REC and MAXLINE were significant. Data from before the transition (plateaus 1 and 2, separately) were compared to the average of data at the transition (plateau 3) and after the transition (plateau 4). Only the contrast between plateau 1 and the average of plateaus 3 and 4 was significant for inphase performance. Both contrasts were significant on %REC and MAXLINE for antiphase performance. For antiphase performance, there was an increase in noise and a decrease in attractor strength from before the transition to transition and after transition levels. Similar trends were apparent for inphase performance, although only one contrast was significant.

Those changes in %REC and MAXLINE were large. Although comparisons across experiments can be only qualitative, the change in %REC, in particular, was 19-34% larger than changes that resulted from relative phase mode (Experiment 1) or frequency asymmetry (Experiments 1 and 2). Figure 18 depicts those more substantial changes in the first three dimensions of sample reconstructed movement (top panels) and breathing (bottom panels) attractors. The data are for a single participant before (0.75 Hz; left panels) and after (1.35 Hz; right panels) a transition from antiphase performance to phase wrapping and intermittency. Although the attractors maintained the same general character, there were clear visual changes in both the movement and breathing attractors from before to after the transition. Unlike the phase wrapping observed in the relative phase measure, the attractors remained bounded, which meant cross recurrence measures could be calculated with relatively low variance across

participants. Values on the cross recurrence measures could, therefore, be summarized across participants using means in the above analyses.

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insert Figure 18 about here.

Discussion

In Experiment 3, there were several indicators that inphase performance was more stable than antiphase performance in motor-respiratory coordination. First and foremost, during familiarization trials, the accuracy of performance was similar for both patterns but the variability of inphase performance was lower than that for antiphase performance. That variability result was consistent with the results of Experiment 1. Participants could also maintain faster frequencies better and there were fewer transitions when they started experimental trials at inphase than at antiphase. Both of those results are indirect indicators that inphase performance was more stable than antiphase performance. Together, those results parallel many observations in interlimb coordination (e.g., Kelso, 1984; Kelso et al., 1986, 1987; Tuller & Kelso, 1989; Yamanishi et al., 1980), which suggests that motor-respiratory coordination and interlimb coordination share relevant dynamical features.

The phase transition paradigm, developed in the context of interlimb coordination (Kelso, 1984), was effective in eliciting transitions in motor-respiratory coordination. Those transitions were not from antiphase toward inphase, as would be predicted for components that are more symmetric like the

index fingers of the left and right hands. Rather, the anticipated phase transitions from both antiphase and inphase toward phase wrapping and intermittent behavior were observed. Those same dynamics have been observed previously within the motor subsystem of the body in coordination between the arms and legs (Kelso & Jeka, 1992) and were predicted based on the asymmetric extension of the HKB model (Fuchs et al., 1995; Kelso et al., 1990; Kelso & Ding, 1993; Kelso & Jeka, 1992; Mitra et al., 1997). As I hypothesized and is consistent with the work of Kelso and Jeka (1992) and von Holst (1973), the incidence of such complex dynamics may have less to do with the particular bodily subsystems involved than with inherent asymmetries in the frequencies of the coordinated components.

Characteristics around phase transitions are remarkably similar regardless of the material substrate in which the transitions occur (Iberall & Soodak, 1978). Critical fluctuations, a distinguishing feature of self-organizing systems, typically occur just before phase transitions (Haken, 1983; Iberall & Soodak, 1978). In the current study, critical fluctuations occurred as indicated by increased noise and decreased attractor strength prior to transitions. Frequency manipulations produced changes in both stochastic and deterministic aspects of variability in interlimb coordination, although the deterministic changes were more pronounced (Richardson et al., 2007). The results of the current study were, therefore, somewhat contrary. However, what constituted a meaningful difference in the magnitude of those changes was not clear in Richardson et al. (2007). Additional work should be done to clarify perhaps focusing on differences in effect size.

In the current study, when participants were instructed to move and breathe at the same frequency at baseline, movement frequency decreased and breathing frequency increased. A unidirectional influence of movement on breathing has been hypothesized (Bramble & Carrier, 1983; Garlando et al., 1985) but those results indicate there was a bidirectional influence. In interlimb coordination, a similar bidirectional influence is observed. For example, skilled musicians have a high degree of dependence between the hands (see Summers, 2000 for a review). That is, each hand cannot be controlled independently when in coordination, despite what is often stated by the musicians themselves. An interesting departure from results in interlimb coordination was that the coupled frequency was closer to the faster characteristic movement frequency. When two pendulums of different lengths (one in each hand) are swung together, the coupled frequency tends to be closer to the characteristic frequency of the slower pendulum (Kugler & Turvey, 1987). Together, those results suggest that components with less inertia, the faster pendulum in interlimb coordination and breathing in motor-respiratory coordination, are more likely to compensate in frequency. The motor-respiratory coordination result indicates that breathing was more flexible than leg movement. The potential significance of that result is that breathing more so than movement might facilitate transitions between motor-respiratory coordination patterns.

Experiment 4: Visual Feedback

Differences in the stability of inphase and antiphase performance in interlimb coordination were initially thought to originate from neural constraints (Haken et al., 1985; Kelso, 1984; Kelso et al., 1986; Yamanishi et al., 1980). Those proposals were based on evidence that shifts from less stable to more stable gaits could be induced through the stimulation of nerves associated with leg movement in cats (Grillner & Zangger, 1979; Shik, Severin, & Orlovskii, 1966). Later evidence of differences in the stability of inphase and antiphase performance from interlimb coordination between-persons (Amazeen, Schmidt, & Turvey, 1995; Schmidt, Carello, & Turvey, 1990; Schmidt & O'Brien, 1997; Schmidt & Turvey, 1994), in which the only link between coordinated components was visual information, suggested perceptual constraints were also important. Preliminary evidence for perceptual constraints has also been identified in motor-respiratory coordination (Gonzales, Hessler, & Amazeen, 2010; Hessler et al., 2010). Given the structural complexity of motor-respiratory coordination, perceptual constraints likely influence relative phase performance within a wider system of natural constraints (one being biomechanical: Bramble & Carrier, 1983; Bramble & Jenkins, 1993) as specified by the HKB model. The purpose of this particular experiment was to further explore possible perceptual constraints using feedback displays. Inspiration for Experiment 4 was gained from two existing experimental methodologies: (1) augmented feedback; and (2) perceptual judgments of simulated coordination patterns.

Perceptual constraints imply that the self-perception of motor and respiratory activity can limit or shape performance. Mechsner, Kerzel, Knoblich, and Prinz (2001) instructed participants to rotate cranks hidden under a table, which resulted in the circling of two flags visible on the tabletop. Participants could easily perform the 4:3 ratio, a pattern that is practically impossible for naïve participants, when circling of the two flags was translated into inphase motion via a gearing mechanism. In an alternate paradigm, various displays in which feedback was reduced to the production of single collective shapes or simpler perceptual structures on a computer screen facilitated difficult relative phase (Amazeen et al., 2008; Hurley & Lee, 2006; Kovacs & Shea, 2010; Lee, Swinnen, & Verschueren, 1995; Tomatsu & Ohtsuki, 2005; Wenderoth & Bock, 2001) and ratio (Gonzales et al., 2010; Hessler et al., 2010; Kovacs, Buchanan, & Shea, 2010; Swinnen, Dounskaia, Walter, & Serrien, 1997) performance.

Interdependence of perception and action in other coordinative activities (e.g., Amazeen et al., 1995; Mechsner et al., 2001; Mitra et al., 1997; Schmidt et al., 1990; Schmidt & O'Brien, 1997; Schmidt & Turvey, 1994) implies that a similar interdependence might exist in motor-respiratory coordination. Evidence from studies in which augmented feedback was utilized provides preliminary support for that hypothesis. In one study, participants performed different coordination patterns with displays in which the compatibility between motor-respiratory coordination and perceptual changes in the displays varied (Hessler et al., 2010). Performance was facilitated by a ball-balloon display in which display features were most compatible with natural movement and breathing

characteristics. Upward-downward motion of the ball was compatible with forward-backward arm movement, whereas inflation-deflation of the balloon was compatible with inhalation-exhalation. In another study, simple ratio performance was more stable than complex ratio performance in motor-respiratory coordination, as specified in a dynamical model called the sine circle map, when participants used displays in which feedback for the performance of different patterns was made to look different but not when that feedback was made to look the same (Gonzales et al., 2010).

In an alternate methodology, participants' perceptual judgments of simulated coordination patterns have been used to demonstrate the constraints of perception on action. Computer simulations were produced in which two balls oscillated side-by-side. Simulations of the most stable relative phase patterns, inphase and antiphase, were judged to be the most coordinated (Bingham, Schmidt, & Zaal, 1999; Bingham, Zaal, Shull, & Collins, 2001) and the least variable (Zaal, Bingham, & Schmidt, 2000). When phase variability (Wilson, Bingham, & Craig, 2003; Zaal et al., 2000) or frequency (Bingham et al., 2001) of the presented relative phase patterns increased, judgments of perceived variability increased, but the steepest increase occurred when participants observed inphase. In a study on ratio perception, participants observed simulated ratios side by side and, in a forced-choice paradigm, judged whether they were the same or different (Gonzales et al., 2010). The most stable ratios performed in interlimb coordination and motor-respiratory coordination like 1:1 and 2:1 were easily distinguished from other less stable ratios (e.g., 3:2, 5:3, and 8:5). Together, those

results suggest that perceived changes were most salient at the most stable coordination patterns in comparison to other less stable relative phases or ratios.

In Experiment 4, I investigated whether displays in which two balls oscillated vertically in a projected image could be used to facilitate motor-respiratory coordination. The main purpose of the experiment was to clarify further whether perceptual constraints influence motor-respiratory coordination. Unlike most previous investigations (Bingham et al., 1999, 2001; Zaal et al., 2000), motion of the balls was not simulated but was controlled directly by participants' movement and breathing (see also Gonzales et al., 2010; Hessler et al., 2010). Inphase and antiphase performance was examined with three different categories of visual feedback: control (no visual feedback), inphase feedback (balls moved up and down together), and antiphase feedback (balls moved opposite each other). Predictions were based on previous feedback results (Amazeen et al., 2008; Roerdink, Peper, & Beek, 2005; Tomatsu & Ohtsuki, 2005). The accuracy of inphase and antiphase performance was expected to be similar in the different feedback conditions but the variability results were expected to be different. The different feedback conditions were expected to impact the variability of inphase performance less because it is already quite stable. Antiphase performance was expected to be more variable in the control feedback condition than the visual feedback conditions and in the antiphase feedback condition than the inphase feedback condition. The impact of feedback on the cross recurrence quantification analysis measures was exploratory but the

expectation was for %REC and MAXLINE to be higher when relative phase performance was more stable.

Method

Participants

Fifteen participants (13 men; 2 women; 18–31 years old) received credit toward their introductory psychology course in exchange for their participation. Exclusion criteria were the same as in Experiment 1. All participants were treated in accordance with the ethical principles of the American Psychological Association.

Apparatus

Task characteristics and data collection were the same as in Experiment 1, except that ankle weights were not used. Also, a concern identified recently is that direct visual feedback from coordinated components can interfere with performance when additional augmented visual feedback is also available (Kovacs et al., 2010; Kovacs & Shea, 2010). Leg movement and chest movement were, therefore, blocked from view with a curtain (de Poel, Peper, & Beek, 2008; Franz, 2004; Verheul & Geuze, 2003).

Feedback display. On certain trials, feedback for leg movement and breathing was provided with a ball display (see Figure 19) that had been programmed in Visual Basic. The display was projected on a wall 3 m in front of participants using a high resolution computer projector. Upward-downward motion of the balls was controlled by breathing (presented in blue to participants, labeled B in Figure 19) and leg movement (presented in red to participants,

labeled M in Figure 19). The horizontal distance between the balls was 40 cm from center to center. Each ball was 15 cm in diameter. Ball excursion occurred along the paths depicted by the vertical dashed lines (range of motion ≈ 100 cm).

insert Figure 19 about here.

Procedure

Baseline procedures were the same as in Experiment 1, except that no baseline trials were performed with ankle weights. During experimental trials, participants were instructed to perform inphase or antiphase (order counterbalanced). Those relative phase patterns were performed in three different visual feedback conditions (order randomized): control, inphase feedback, and antiphase feedback. There were two 60 s trials per relative phase pattern for each visual feedback condition. Duplicate trials were collected to ensure there was at least one analyzable trial per condition. The frequency for all trials was prescribed at 0.54 Hz (the mean observed when participants were asked to move and breathe at the same frequency during the coupled baseline trial in Experiment 3). A minimum 30 s rest was provided between each trial to minimize fatigue. More rest was provided upon request.

Participants used the ball display in the visual feedback conditions (inphase feedback and antiphase feedback). For inphase feedback and antiphase feedback, participants were instructed to move the balls up and down together or opposite each other, respectively. Regardless of the required relative phase, if

performed properly, then the balls maintained one of those feedback orientations. That was not achieved through a computer programming manipulation but by changing which side of the pneumotachometer was attached to the facemask. Participants were instructed to monitor motion of the balls throughout each trial. The experimenter supervised each participant to ensure that instruction was followed. If not, then the trial was stopped and re-run.

Calculations, Dependent Measures, and Design

Calculations and dependent measures were the same as in Experiment 1. Unless otherwise noted, dependent measures from the second trial in each condition were analyzed with 2 (Pattern: inphase and antiphase) x 3 (Visual Feedback: control, inphase feedback, and antiphase feedback) ANOVAs. Both Pattern and Visual Feedback were within-subjects factors.

Results

Frequency

Table 11 identifies preferred movement and breathing frequency and the variable error of movement and breathing frequency observed for baseline trials. Consistent with the results of Experiments 1–3, the preferred movement frequency was much faster than the preferred breathing frequencies, which reflects their natural asymmetry. One-way ANOVAs were performed comparing performance in the resting and loaded conditions on the dependent measures breathing frequency and the variable error of breathing frequency. Again, consistent with the results of the other experiments, the ANOVA on breathing frequency was not significant, $F(1, 14) = 0.80$, $p = .39$, $\eta^2 = .05$, but the ANOVA

on the variable error of breathing frequency was significant, $F(1, 14) = 9.34$, $p < .01$, $\eta^2 = .40$. The mean resting and loaded breathing frequencies were similar but the variability of the resting breathing frequency was lower than the variability of the loaded breathing frequency.

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insert Table 11 about here.

Experimental manipulation checks. Analyses were performed to determine whether or not movement and breathing frequency were maintained at 0.54 Hz and in a monofrequency relation during experimental trials. Movement frequency, breathing frequency, and their frequency ratio were collapsed across Pattern and Visual Feedback because effects on those factors were not significant in ANOVAs. Movement frequency and breathing frequency were compared to a test value of 0.54 Hz in t-tests. The effects on both movement frequency, $t(14) = 2.85$, $p < .05$, and breathing frequency, $t(14) = 3.00$, $p < .05$, were significant. Movement ($M = 0.568$ Hz, $SD = 0.039$ Hz) and breathing ($M = 0.570$ Hz, $SD = 0.038$ Hz) frequencies were slightly faster than the prescribed pace. A t-test in which the frequency ratio was compared to 1.00 was not significant, indicating that participants maintained a monofrequency relation ($M = 1.000$, $SD = 0.003$) between movement and breathing.

Relative Phase

Figure 20 depicts the constant error (top panel) and variable error (bottom panel) of relative phase performance in the different feedback conditions for

inphase (filled bars) and antiphase (open bars) performance. ANOVAs were performed on constant error and variable error. There were no significant effects on constant error. Breathing led movement (constant error was negative) but the lead was similar across conditions. The main effect of Visual Feedback on variable error was significant, $F(2, 28) = 16.85$, $p < .001$, $\eta^2 = .55$, but the main effect of Pattern was not significant. Main effect contrasts performed between each level of Visual Feedback were all significant (control vs. inphase feedback: $F(1, 14) = 66.23$, $p < .001$, $\eta^2 = .83$; control vs. antiphase feedback: $F(1, 14) = 6.75$, $p < .05$, $\eta^2 = .33$; inphase vs. antiphase feedback: $F(1, 14) = 6.78$, $p < .05$, $\eta^2 = .33$). Real-time feedback decreased the variability of relative phase performance, and that variability was lower with inphase feedback than antiphase feedback.

insert Figure 20 about here.

Cross Recurrence Quantification Analysis

The attractor reconstruction and cross recurrence quantification analysis parameters used were the same as in Experiment 1. The time delay used for attractor reconstruction, 24 data points, approximated that obtained from the average mutual information function (M = 23.28 data points; SD = 0.17 data points). Movement and breathing data were embedded in five dimensions. That dimensionality approximated the average estimate from false nearest neighbors analysis (M = 5.07 dimensions; SD = 0.32 dimensions). Data were considered

cross-recurrent if they were within 21% of the mean distance of the reconstructed attractor. Figure 21 depicts %REC (top panel) and MAXLINE (bottom panel) in the different feedback conditions for inphase (filled bars) and antiphase (open bars) performance. The results of ANOVAs performed on %REC and MAXLINE, identified in Table 12, will be discussed next.

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insert Figure 21 and Table 12 about here.

The main effect of Pattern was significant on %REC and marginally significant on MAXLINE. Across feedback conditions, %REC and MAXLINE were higher for inphase performance than antiphase performance. The main effects of Visual Feedback on %REC and MAXLINE were also significant. Only the contrasts between inphase feedback and the other feedback conditions were significant. Both %REC and MAXLINE were lower for inphase feedback than the other feedback conditions, indicating that there was an increase in noise and a decrease in attractor strength when inphase feedback was utilized. To visualize those changes, cross recurrence plots for a single participant performing the antiphase pattern with inphase feedback (left panel) and antiphase feedback (right panel) are presented in Figure 22. The plot for inphase feedback was more mottled than the plot for antiphase feedback, indicating that there were more changes on short time scales with inphase than with antiphase feedback.

insert Figure 22 about here.

Discussion

The results of Experiment 4 demonstrate that perceptual constraints are active in and influence motor-respiratory coordination. Feedback helped for both inphase and antiphase performance. Relative phase variability was significantly lower in the augmented feedback conditions than in the control condition. The effect on inphase performance differed from previous interlimb coordination results in which augmented feedback only facilitated the performance of more difficult patterns (between 90° and 180°, Amazeen et al., 2008; 90° and 270°, Tomatsu & Ohtsuki, 2005). An advantage of augmented feedback in addition to naturally available feedback for antiphase performance is consistent with that advantage in unimanual tracking (Bogaerts, Buekers, Zaal, & Swinnen, 2003; Roerdink et al., 2005). In terms of accuracy and/or variability, that advantage likely arises from a more salient visual representation of relative timing information (Gonzales et al., 2010; Hessler et al., 2010). Specifically, that information is more salient with inphase and antiphase feedback than with naturally available feedback during spontaneous performance.

Motor-respiratory coordination also differed between the two augmented feedback conditions. For both inphase and antiphase performance, relative phase variability was significantly lower with inphase feedback than with antiphase feedback. The advantage of inphase feedback over antiphase feedback has been

observed previously in interlimb coordination (Amazeen et al., 2008) and unimanual tracking tasks (Bogaerts et al., 2003; Roerdink et al., 2005; Ryu & Buchanan, 2009). Inphase feedback forms a coherently grouped visual motion structure (Bogaerts et al., 2003; Roerdink et al., 2005; Ryu & Buchanan, 2009), which has been identified as a perceptual Gestalt (Johansson, 1950). Such coherent visual information makes mismatches between coordinated components salient (Tomatsu & Ohtsuki, 2005), which participants can perceive (Bingham et al., 2001; Wilson et al., 2003; Zaal et al., 2000). Examples of possible mismatches identified in perceptual research include changes in phase variability and oscillation frequency. Both of those changes were likely relevant in the current study.

The cross recurrence results provide some preliminary evidence that such variability and frequency information could be used for online control in motor-respiratory coordination. To my knowledge, this is the first use of any recurrence analysis procedure to examine feedback in coordination. Compared to performance in the control condition and with antiphase feedback, noise was higher and attractor strength lower with inphase feedback. While that evidence might normally indicate that inphase feedback was a disadvantage, recall that inphase feedback facilitated relative phase performance more than the other feedback conditions. Thus, higher noise and lower attractor strength could indicate that small within-cycle trajectory changes (e.g., a quick jerk in leg movement) were used to achieve more stable relative phase patterns. The difference in the patterning of cross recurrence for inphase feedback and

antiphase feedback in Figure 22 supports that interpretation. Such changes were on a fast enough time scale that they were not likely a conscious action on the part of each participant.

A difference between the results of this experiment and the results of Experiments 1 and 3 was that variable error was similar for inphase and antiphase performance. In this experiment, unlike in those previous experiments, direct visual feedback of leg and chest movement was blocked from view, which suggests that differences in relative phase variability could result from visual perception. There were, however, differences in the structure of coordinative variability. Noise was lower and attractor strength marginally higher for inphase performance compared to antiphase performance. That result was in partial support of the results in Experiment 1 (a quantitative comparison could not be made in Experiment 3). In interlimb coordination, differences in inphase and antiphase performance were found to result from changes in attractor strength alone (Richardson et al., 2007). As identified by others (Amazeen et al., 2008; Tomatsu & Ohtsuki, 2005), differences in performance with the same augmented feedback suggest that physiological constraints are still an important consideration. Participants were sufficiently attuned to their body's natural tendencies to control their action, even to the extent that control required synchronization across multiple physiological subsystems of the body.

GENERAL DISCUSSION

The inherent frequency asymmetry between movement and breathing was of central importance in the current study. It prevented performance of the perfect inphase and antiphase patterns across experiments and was the basis of the complex dynamics observed in Experiment 3. In all of the experiments, breathing tended to lead movement. Those results were consistent with observations in coordination between breathing and wrist movement (Temprado et al., 2002) and indicated that the oscillator of slower natural frequency led the oscillator of faster natural frequency. Therefore, oscillators with less inertia, not a faster frequency (e.g., Rosenblum & Turvey, 1988; Turvey et al., 1986), might tend to lead (i.e., shorter, lighter pendulums in interlimb coordination; breathing in motor-respiratory coordination). A lead of the component with less inertia could facilitate transitions, which have been identified as important for flexibility during motor-respiratory coordination (Garlando et al., 1985). For example, breathing could be harnessed quickly to make a switch from one pattern to another while leg movement lags. That hypothesis is consistent with the observation that breathing can induce changes in the stride frequency during walking (Raßler & Kohl, 2000).

A tendency for breathing to vary more in frequency or phase than movement has been taken as evidence that movement has more of an influence on breathing than vice versa. For example, in the motor-respiratory coordination literature, a unidirectional influence of movement on breathing has been hypothesized (e.g., Bramble & Carrier, 1983; Garlando et al., 1985) and coupling between movement and breathing has been modeled as unidirectional

(Daffertshofer et al., 2004). Because one component is more likely to vary in frequency or phase does not necessarily indicate that the influence from the other component is larger. Such variation could be interpreted differently. Breathing, being the component with less inertia, could simply be more flexible than movement. That proposition is consistent with the result in Experiment 3 in which the change in breathing frequency was larger than the change in movement frequency from uncoupled to coupled baseline trials.

Asymmetry and the Breathing Lead

The use of ankle weights in Experiments 1 and 2 was inspired by the wrist-pendulum paradigm (Kugler & Turvey, 1987; Rosenblum & Turvey, 1988). That methodology proved useful for a controlled investigation of frequency asymmetry in motor-respiratory coordination. Heavier ankle weights produced natural movement frequencies that more closely approximated the natural breathing frequency. Still, even with the heaviest weight (slowest leg), the frequency asymmetry between movement and breathing remained substantial (M = 0.32 Hz). At a comfortable oscillation frequency, when additional weight was added to the leg, performance more closely approximated the true inphase and antiphase patterns (the breathing lead decreased). That effect was replicated in two experiments for inphase performance at a comfortable frequency but was not replicated at a fast frequency. In interlimb coordination, changes in the degree of approximation have been lawfully related to a ratio of the natural frequency characteristics of each component (Rosenblum & Turvey, 1988; Turvey et al., 1986, 1988), a collective measure spanning the components.

The natural frequency of a pendulum-like component can be derived directly from its physical characteristics and is a function of its length and mass (Kugler & Turvey, 1987). That ability to identify natural frequencies is one reason why wrist-pendulum studies are so well-controlled. That quantity can be derived for the motor component in motor-respiratory coordination (leg movement in the current study; e.g., Dempster, 1955) but the natural breathing frequency can only be estimated empirically. Additional modeling is needed to accurately identify the characteristic breathing frequency. It is likely to be related to a quantity like tidal volume, the volume of air displaced between inhalation and exhalation at rest. My expectation is that relative phase approximation in the current study was related to the ratio of characteristic movement and breathing frequencies in which breathing, the component with a slower natural frequency but less inertia, leads. Variability in the empirical estimation of breathing frequency did not permit such modeling in the current study.

Characteristic frequencies do not preclude the performance of other frequencies. The motor and respiratory subsystems are dynamical systems that can be softly assembled, that is, assembled temporarily and for a functional purpose in line with the particular physiological, neurological, and/or informational constraints at the time (Kugler & Turvey, 1987; Prigogine, 1967; Thelen & Smith, 1994; Turvey et al., 1986). Being softly assembled, motor-respiratory coordination also exhibited complex dynamics like phase wrapping and intermittency. Soft-assembly can be contrasted with hard-wiring, the argument that rigidly determined neural pathways correspond to each behavior

that is observed (e.g., Grillner & Zangger, 1979; Selverston, 1980; Shik et al., 1966). Soft-assembly allows the flexibility necessary for a range of coordination patterns and frequencies to be performed. Consider the various frequencies of movement exhibited by horses. Although a horse's legs are built to maintain a particular frequency best (related to each leg's length and mass), leg movement can be softly-assembled to maintain different frequencies (Hoyt & Taylor, 1981). In locomotion, the consequence is different gaits. Similarly, in motor-respiratory coordination, the consequence is different frequency ratios.

At the faster frequency in Experiment 2, as frequency asymmetry decreased, performance drifted away from the intended inphase pattern. That accuracy result was opposite to the accuracy results at the slower frequency in Experiment 1 and was a surprise because it was opposite to the accuracy predictions of the HKB model (Kelso et al., 1990) and the observations in interlimb coordination (e.g., Rosenblum & Turvey, 1988; Turvey et al., 1986). The accuracy result at the faster frequency could be related to changes in the spring-like properties of leg movement (Turvey, 1990; Turvey et al., 1988), which could be examined in future research using Hooke's portraits (Mottet & Bootsma, 1999). Muscles and other tissues in the leg can act like a spring, making leg movement elastic. As Turvey (1990) outlined, that elasticity can vary with movement frequency. Data on the locomotion of quadrupeds in the Serengeti (Pennycuick, 1975) indicated that the relation of elasticity to a gravitational constant depended on movement frequency. In the current study, it is possible that the elasticity of leg movement decreased at the faster frequency. If that was the

case and the elasticity of breathing remained constant, then movement would lag in its cycle relative to breathing, accounting for the observed accuracy result. The results indicated, however, that any change in the stiffness of leg movement was accompanied by a large frequency asymmetry. As frequency asymmetry is a product of coupled components, it is possible that change in the elasticity of leg movement is not the only relevant piece, but that a change in the elasticity of coupling between movement and breathing also occurred.

Asymmetry and Variability

According to the HKB model (see Equation 1; Haken et al., 1985; Kelso et al., 1990), relative phase and variability are correlated: performance that more closely approximates inphase and antiphase is predicted to be less variable. In Experiment 1, the opposite effect was observed: performance that more closely approximated inphase and antiphase was more variable. That effect was not replicated for inphase performance in Experiment 2, which might have resulted from a carry-over effect from the faster to slower frequency condition (a faster frequency trial with one mass preceded a slower frequency trial with another mass) or a less effective frequency asymmetry manipulation. In either case, the influence of frequency asymmetry on relative phase accuracy was reduced, which could render a smaller but not an opposite pattern of change in variability. Clarification of those results is needed but the results of Experiment 1 were an interesting departure from the results of most wrist-pendulum studies (e.g., Amazeen et al., 1996, 1998a; Schmidt et al., 1993; Sternad et al., 1992, 1996; Treffner & Turvey, 1995; Turvey et al., 1986).

A similar relation between accuracy and variability to that observed in Experiment 1 has been observed previously when symmetry was broken (Amazeen et al., 1997, 1998b; Mulvey et al., 2005), indicating that relation is a property of inherently asymmetric systems. To account for different relations between accuracy and variability, researchers have used an extension of the HKB model originally developed to account for intricacies in coordination between the hands (Treffner & Turvey, 1995, 1996):

$$\dot{\phi} = \Delta\omega - [a\sin(\phi) + 2b\sin(2\phi)] - [c\cos(\phi) + 2d\cos(2\phi)] + \sqrt{Q}\zeta_t \qquad (3).$$

In Equation 3, the fundamental coordination dynamics are broken by two additional 2π periodic terms, $c\cos(\phi)$ and $2d\cos(2\phi)$, representing the body's functional asymmetry. The values of *c* and *d* are generally smaller than *a* and *b*. That reflects the roles of *a* and *b* in determining the fundamental dynamics of the inphase and antiphase attractors, and *c* and *d* in modulating those dynamics.

The nature of the functional asymmetry expressed by *c* and *d* is not clear at present. In past work, *c* has been linked to manipulations of shared cognitive activity (Pellecchia et al., 2005; Shockley & Turvey, 2005) and *d* has been linked to handedness (Amazeen et al., 1997; Treffner & Turvey, 1995, 1996) and directed attention (Amazeen et al., 1997). In general, *c* and *d* are modeled separately: one term is set to zero and the other term is manipulated. The manipulation of each term produces different predictions. For a decrease in the magnitude of *c*, fixed point shift is predicted to increase with little change in variability (Pellecchia et al., 2005). For an increase in the magnitude of *d*, fixed

point shift is predicted to increase with a decrease in variability (Amazeen et al., 1997). Thus, the inverse relation between accuracy and variability observed in motor-respiratory coordination can be modeled by using *d* and setting *c* to zero, although the exact nature of the functional asymmetry that is captured by *d* about movement and breathing is unclear.

That relation between accuracy and variability may be related to the degree to which the functional asymmetry of coordination is modulated to match the typical circumstances for a task. In the wrist-pendulum paradigm, frequency asymmetry between the left and right hands is induced through the coordination of pendulums of different lengths and masses. The frequency asymmetry in motor-respiratory coordination is, by contrast, inherent. Across exercises, the natural frequency of movement is generally faster than that of breathing (e.g., Amazeen et al., 2001; Bernasconi & Kohl, 1993; Bramble & Carrier, 1983; Garlando et al., 1985; Mahler, Hunter, et al., 1991). In the current study, the inherent frequency asymmetry between leg movement and breathing was substantial (M = 0.32 Hz in the heaviest weight condition). Even in rowing (Mahler, Hunter, et al., 1991), the exercise in which the natural movement frequency is closest to the natural breathing frequency, those frequencies are still quite asymmetric. Considering together the results in motor-respiratory coordination and the wrist-pendulum studies, relative phase variability increases the more performance deviates from normal conditions. To further examine that conclusion, frequency asymmetry in another inherently asymmetric system like coordination between the arms and legs should be manipulated systematically.

A result from Experiment 1 that provides some support of that conclusion was that inphase performance better approximated the naturally detuned state than did antiphase performance when the natural frequencies of movement and breathing were most asymmetric. That finding and the variability findings can be considered evidence in contradiction to the traditional view that different natural frequencies be considered in competition with each other (von Holst, 1973), each component wanting to maintain its characteristic frequency, but being pulled toward the characteristic frequency of the other component. Although complex dynamics like phase wrapping and intermittency are likely an inherent property of systems with frequency asymmetry (Jeka & Kelso, 1995; Kelso & Jeka, 1992), the existence of such complex dynamics is not necessarily synonymous with frequency competition. The term frequency competition also implies that there are two competing frequency components. It is more accurate to describe a single virtual frequency that is established through the interaction of coordinated components (Turvey et al., 1986). That single virtual frequency cannot be reduced to the properties of either component in isolation but emerges as a property of the compound system.

In the establishment of a virtual frequency, the two pendulum-like components should not be considered welded together through a rigid connection so that they behave as one. Rather, the connection between pendulums is more like a spring (Turvey, 1990). That is because there is no rigid mechanical connection between rhythmic movements in the human body (Kugler & Turvey, 1987), as can also be said for movement and breathing. The connections within

the motor subsystem and between the motor and respiratory subsystems of the body are anatomical, neuromuscular, and/or informational. Insofar as coordination is exhibited within or between subsystems, that coordination should be considered temporary and functionally related to the constraints at the moment. For example, infant stepping can be suppressed or elicited through the addition of mass to the legs and the submerging of the legs in water, respectively (Thelen, 1989; Thelen & Fisher, 1982; Thelen & Smith, 1994). Variety in the patterns of coordination observed is necessary for behavioral flexibility and is facilitated through soft-assembly of the coordinated components.

Motor-respiratory coordination, like interlimb coordination (e.g., Kugler & Turvey, 1987; Richardson et al., 2007; Turvey et al., 1986), cannot be understood by describing the details of the underlying components (e.g., metabolic processes, neurons, muscles). In fact, such reduction would complicate an understanding of motor-respiratory coordination for two reasons (Kelso, Holt, Kugler, & Turvey, 1980; Kugler, Kelso, & Turvey, 1980): (1) there are too many degrees of freedom associated with the microscopic aspects of those bodily subsystems for which to account; and (2) the interconnectedness of those subsystems and nonlinear interactions between them makes the coordination whole different from the sum of the parts. Consistent with the synergetics approach and the behavior of self-organized systems (Haken, 1983), a lower-level description can be replaced by a simpler unitary description, a macroscopic property of the coordinative structure (Bernstein, 1967), that reflects the behavior of each underlying part but spans them (Kelso et al., 1980; Kugler et al., 1980;

Turvey et al., 1986). The ratio of characteristic frequencies represents one such property, and the dependent measures used in this study, relative phase, %REC, and MAXLINE, reflect that same spirit.

Soft Constraints on Relative Phase

In the current study, there were many indications that inphase was more stable than antiphase performance. Like previous studies in the interlimb coordination literature (e.g., Kelso, 1984; Yamanishi et al., 1980), relative phase variability was lower for inphase than antiphase performance in two experiments. Although relative phase mode influenced attractor strength alone in interlimb coordination (Richardson et al., 2007), in the current study, there was evidence that inphase was both less noisy and higher in attractor strength than antiphase. An additional indirect indicator that inphase was more stable than antiphase performance was that transitions from inphase occurred less often than from antiphase. The implication is that soft constraints on motor-respiratory coordination rendered exhaling with forward movements and inhaling with backward movements (inphase) more stable than inhaling with forward movements and exhaling with backward movements (antiphase). Anatomically, it might be easier to inhale fully when the leg moves backward and the abdominal muscles are relaxed (but it is not a neural requirement). That difference in stability suggests runners would tend to anchor inhalations with the stance phase, when the foot contacts the ground, as opposed to the swing phase, when the leg is moving forward. That exact tendency to inhale with the stance phase has been observed previously during human running (Bramble & Carrier, 1983).

Consistent with its structural complexity, any one of very many underlying components has the potential to influence motor-respiratory coordination. A soft constraint identified in Experiments 1, 2, and 3 was frequency asymmetry. Another soft constraint is the visceral piston mechanism (Bramble & Carrier, 1983; Bramble & Jenkins, 1993) in which inertial oscillations from, for example, footfalls impose limits (but not requirements) on respiration such that breathing becomes entrained with movement. Previous studies in interlimb coordination revealed that inphase and antiphase were stable coordination patterns between people in which the only link was visual information (Amazeen et al., 1995; Schmidt et al., 1990; Schmidt & O'Brien, 1997). Augmented feedback in which more complex movement trajectories were translated into a simpler perceptual motion on a computer screen was an advantage over naturally available feedback alone (Amazeen et al., 2008; Bogaerts et al., 2003; Roerdink et al., 2005; Tomatsu & Ohtsuki, 2005). The possibility that perception is a soft constraint on motor-respiratory coordination was explored in Experiment 4.

Participants performed the inphase and antiphase patterns in different feedback conditions. In two real-time feedback conditions, relative phase performance was translated into inphase or antiphase motion between two vertically oscillating balls on a computer screen. That is, feedback was augmented and straightforward. In Experiment 4, consistent with previous results in interlimb coordination (Amazeen et al., 1995, 2008; Schmidt et al., 1990; Schmidt & O'Brien, 1997; Tomatsu & Ohtsuki, 2005), there was a dependence of motor-

respiratory coordination on perception (see also Gonzales et al., 2010; Hessler et al., 2010). Relative phase variability was reduced when real-time feedback was provided and minimized when that real-time feedback depicted inphase motion as opposed to antiphase motion. Together, those results suggest that motor-respiratory coordination benefited from a more salient visual representation in which changes in performance were apparent. However, coordination benefited most from inphase feedback, when that visual representation formed the most coherently grouped motion structure (Bogaerts et al., 2003; Roerdink et al., 2005; Ryu & Buchanan, 2009). Johansson (1950) called that coherent structure a perceptual Gestalt.

Manipulations of visual information in both phase variability (Wilson et al., 2003; Zaal et al., 2000) and frequency (Bingham et al., 2001) have been shown to affect the perception of different relative phase patterns. Those changes in timing information were easiest to pick up when inphase motion was presented (Bingham et al., 1999, 2001; Zaal et al., 2000). The ball display used in the current study was very similar to the displays presented to participants in those perception studies. Participants presumably utilized the phase variability and frequency information in the ball display to identify mismatches between the timing of movement and breathing. In support of that conclusion, relative phase variability was minimized when the balls moved in an inphase motion but noise was also higher and attractor strength was lower than in the other feedback conditions. That result indicates that more stable relative phase patterns were

achieved through small, within-cycle trajectory changes such as very quick jerks in leg movement.

A limitation regarding studies that involve augmented feedback is that systems become functionally different when feedback is present. For example, in a complex unimanual tracking task, individuals relied on augmented feedback to such an extent during practice that upon its removal, performance deteriorated (Schmidt & Wulf, 1997). Therefore, it is difficult to conclude with certainty that changes resulting from manipulations of visual perception in Experiment 4 reflect the same perceptual constraints involved in spontaneous motor-respiratory coordination during exercise. Facilitation of motor-respiratory coordination through visual perception demonstrates with more certainty that perceptual constraints can influence or pervade motor-respiratory coordination.

Coordination was Relative

At slower oscillation frequencies, behavior approximated the stable inphase and antiphase patterns. As oscillation frequency increased, behavior transitioned into a phase wrapping regime, visiting all possible relative phases in a running sequence. Those complex dynamics were often intermittent in which behavior was attracted to inphase and antiphase for extended periods of time compared to other relative phases. Typically, transitions are toward new, more energetically-favorable modes (e.g., Hoyt & Taylor, 1981; Kelso, 1984). Whether or not phase wrapping is energetically more favorable is not clear from the current results or previous theory. Nicolis and Prigogine (1977) proposed that dissipative structures allow for the most efficient energy use. Dissipative structures are

complex dynamical structures that form spontaneously and can be reproduced under similar conditions. It is possible that phase wrapping, even though it is infinitely unstable, is a dissipative structure. Whether that regime was more energetically favorable than maintaining stable relative phase patterns at high frequencies could be examined in future research by recording of oxygen consumption.

Those results were consistent with predictions of the asymmetric extension of the HKB model in which a detuning term, $\Delta\omega$, accounting for frequency asymmetry was included (Fuchs et al., 1995; Kelso et al., 1990; Kelso & Ding, 1993; Kelso & Jeka, 1992; Mitra et al., 1997). When the magnitude of the detuning term is very large, negatively-sloped zero crossings are eliminated. The result is that stationary solutions no longer exist, only running solutions, and intermittency is reflected as changes in the derivative at different values of relative phase. While the inverse relation between accuracy and variability could be accounted for using the *d* term in Equation 3, that term does not account for phase wrapping and intermittency. That is because changes in *d* do not shift the HKB function up and down, but modulate the function, while it remains centered around a relative phase derivative of zero. The need to use both $\Delta\omega$ and *d* suggests that there are multiple asymmetric influences in motor-respiratory coordination.

Complex dynamics, including both phase wrapping and intermittency, have also been observed previously in the coordination of arm and leg movement (Jeka & Kelso, 1995; Kelso & Jeka, 1992). Such observations led Kelso and Jeka

(1992) to suggest that some of the most interesting dynamics arise when the symmetry between coordinated components is broken. A major source of asymmetry between the arms and legs, movement and breathing, and the fins of fish, is the natural frequency difference between the components. That source of asymmetry makes the complex dynamics exhibited in those disparate physiological systems quite similar. Another source of asymmetry is a functional asymmetry, like what makes the left and right hands different (Amazeen et al., 1997; Treffner & Turvey, 1995, 1996). Functional asymmetry can lead to unusual relationships between accuracy and variability, which again, appear in different dynamical systems from interlimb coordination to motor-respiratory coordination.

The dynamics observed in motor-respiratory coordination and coordination between the arms and legs, like phase wrapping and intermittency, have been referred to as behavioral complexity (Haken, 1983; Kelso, 1995). In the traditional approach, complexity in human behavior is assumed to arise from cognitive mechanisms (e.g., Chomsky, 1965; Fodor, 1975). A particularly prominent example was the explanation for the generativity of human language (Chomsky, 1965). It is important to consider whether that approach results in a description of the same phenomenon at a different level. Another consideration is whether anything is gained because cognitive mechanisms can be equally or more complex. In trying to grasp the origins of behavioral complexity, it is helpful to consider less cortically-evolved animals like von Holst's (1973) fish or physical systems like Rayleigh-Bénard convection. For such systems, there is less of an inclination to conceive of an internal controller or blueprint that governs the

behavioral complexity observed (Kugler & Turvey, 1987; Solé & Goodwin, 2000).

In the coordination of fish fins, von Holst (1973) observed the interaction of two competing tendencies: the magnet effect and the maintenance tendency. Based on those observations, von Holst postulated that there were two different types of coordination. If the magnet effect dominated, then absolute coordination was exhibited in which the fins moved at the same frequency and in a constant phase relation. In Experiment 3, when each participant was instructed to synchronize movement and breathing, an intermediate frequency was elected. However, the latter aspect of absolute coordination, a constant phase relation, was not observed. The relative phase patterns were neither constant nor at the perfect inphase or antiphase patterns. The phase wrapping and intermittent dynamics observed in the current study were more consistent with a dominance of the maintenance tendency and the presence of relative coordination.

Behavioral complexity, like other instances of complexity, such as in human cognitive processes (Van Orden, Holden, & Turvey, 2003), can arise through a simple synergetic explanation (Haken, 1983). Similar to Rayleigh-Bénard convection, simple and local interactions among those very many underlying parts involved in motor-respiratory coordination produce macroscopic patterns at certain values of the control parameter, oscillation frequency. Those macroscopic patterns like phase wrapping and intermittency are observed in the collective order parameter, relative phase. In turn, those macroscopic patterns constrain the behavior of the individual nerves, muscles, and metabolic processes

across larger physiological scales than was possible at lower frequencies. From the synergetics perspective, it becomes clear that behavior is of a holistic, multi-level nature. Behavior of the entire motor-respiratory system is reflected in the simpler, higher level order parameter.

It is important to note that there was nothing inherent about frequency that directed or provided a blueprint for the switches from antiphase or inphase to phase wrapping and intermittency. Control parameters like frequency are non-specific (Kelso et al., 1987; Schöner et al., 1986; Thelen & Smith, 1994). The connection between the control parameter and order parameter became clear only after a phase transition was observed. As long as the system is open and far-from-equilibrium (Babloyantz, 1986; Kelso et al., 1987; Schöner et al., 1986; Turing, 1952), all that is needed for change is instability (Kelso, 1995). Think of the jostling necessary to dislodge a ball stuck in the bottom of a bowl. Once the ball clears the edge of the bowl, it can easily enter into another. In Experiment 3, there was evidence from cross recurrence quantification analysis that dynamical variability increased just prior to transitions. Critical fluctuations, a spike in variability just prior to a phase transition (Kelso et al., 1987; Schöner et al., 1986), are a hallmark of self-organized systems and are observed over a wide variety of systems with different material substrate (Haken, 1983; Iberall & Soodak, 1978). A central principle of dynamical systems theory is that systems with different material substrate often display similar patterns of change.

Traditionally, changes in variability were ascribed to differences in attractor strength alone and noise was assumed to be constant across coordination conditions (e.g., Haken et al., 1985). Although more research is necessary, the influences on %REC in the current study coupled with previous findings in interlimb coordination (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005, 2006) suggest that the assumption of constant noise is often violated. Variation in noise has implications for modeling in which certain nonlinear predictions derived from the HKB model can be slightly incorrect (Riley et al., 2001). Attributing differences in performance to changes in the attractor dynamic alone, therefore, may be incomplete (Riley & Turvey, 2002), and that attribution is agnostic to whether differences at a macroscopic level can originate from underlying degrees of freedom.

The overarching goal was to better understand the nature of variability in motor-respiratory coordination through the use of dynamical measures of variability like those from cross recurrence quantification analysis. The challenge was to differentiate stochastic from deterministic sources of variability (i.e., variability considered a function of the underlying degrees of freedom that support coordination from that which arises at the macroscopic level of coupled oscillators; Fuchs & Kelso, 1994; Riley et al., 2001; Schmidt & Turvey, 1995). In the current study, it was difficult to differentiate between those two sources of variability because the measures meant to reflect those aspects of performance changed in unison. A similar pattern of results has been observed previously in

interlimb coordination with changes in frequency asymmetry (Richardson et al., 2007). Together, those results can be considered partial support for the hypothesis that changes in characteristics like frequency asymmetry might also rescale the magnitude of noise (Richardson et al., 2007). That is, stochastic and deterministic sources of variability might not be completely separable in the biology. However, the cross recurrence measures are correlated, as an increase in patterning implies an increase in recurrence.

Manipulations of relative phase mode, oscillation frequency, and frequency asymmetry in the current study influenced both %REC and MAXLINE. In no case did a manipulation influence one of those measures and not the other. The relative phase mode result, in particular, in which inphase was higher than antiphase in %REC and MAXLINE, deviated from evidence in interlimb coordination in which inphase was higher than antiphase in only MAXLINE (Richardson et al., 2007). Those divergent results could reflect differences in motor-respiratory coordination and interlimb coordination. However, the similar phase wrapping and intermittent dynamics in Experiment 3 and in coordination between arm and leg movement (Kelso & Jeka, 1992) provides evidence against that conclusion. Each manipulation, as in the previous interlimb coordination work, was expected to have a particular connection to stochastic and/or deterministic aspects of performance. That the same independent variables had different effects here suggests that additional work should be done to further clarify the link between cross recurrence measures and different components of variability. One possibility is that the effects of variables like

relative phase mode and oscillation frequency on cross recurrence measures are different in systems with inherent frequency asymmetry.

Clarification of the link between cross recurrence quantification analysis measures and different aspects of variability is an important future direction, and some work has been done in interlimb coordination research toward that goal (Pellecchia et al., 2005; Richardson et al., 2007; Shockley & Turvey, 2005, 2006). The current study and work on postural control (e.g., Riley, Balasubramaniam, & Turvey, 1999) are important because they can be used to assess the generality of that link to other systems. The use of other dynamical systems techniques might also help to provide further clarification. One measure that should be explored in future research is the largest Lyapunov exponent (e.g., Rosenstein, Collins, & De Luca, 1993), the maximal exponential rate of divergence of neighboring trajectories. That measure of dynamical variability should vary inversely with MAXLINE and, therefore, could provide some converging evidence as to what changes in MAXLINE reflect. However, others have cautioned (Riley & Turvey, 2002), and it is important to reiterate, that different dynamical techniques should not be applied just because they exist; their application should always be connected to theory.

Conclusion

The fact that modeling and theory from interlimb coordination can apply to motor-respiratory coordination suggests that interlimb and motor-respiratory coordination share relevant dynamical properties despite differences in physiological substrate. The complex dynamics exhibited in motor-respiratory

coordination were remarkably similar to those observed in coordination between the arms and legs (Kelso & Jeka, 1992). That similarity was related to a frequency asymmetry between the components involved in both those types of coordination. Moreover, perceptual constraints in motor-respiratory coordination were identified that were consistent with previous observations in interlimb coordination (Mechsner et al., 2001; Schmidt et al., 1990). Motor-respiratory coordination results deviated from interlimb coordination results in that the variability of coordination tended to decrease with a larger frequency asymmetry. That result might reflect the natural frequency asymmetry between movement and breathing across exercises. Overall, the coordination dynamics approach (c.f., Kelso, 1995), developed in the context of interlimb coordination, led to several insights and novel results in this between-systems coordination task.

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Table 1

Preferred Mean Movement and Breathing Frequency (Hz) and the Variable Error of Movement and Breathing Frequency (Hz) at Baseline in Experiment 1

	Mean (*SD*)	Variable Error (*SD*)
Movement Frequency		
0 kg	0.679 (0.093)	0.021 (0.006)
1 kg	0.675 (0.057)	0.015 (0.003)
3 kg	0.634 (0.054)	0.016 (0.005)
5 kg	0.618 (0.047)	0.015 (0.007)
Breathing Frequency		
Resting	0.285 (0.053)	0.027 (0.009)
Loaded		
0 kg	0.290 (0.062)	0.045 (0.025)
1 kg	0.297 (0.060)	0.043 (0.017)
3 kg	0.297 (0.065)	0.040 (0.022)
5 kg	0.294 (0.067)	0.043 (0.019)

Table 2

Decomposition of the Pattern x Mass Interaction for the Cross Recurrence Quantification Analysis Measures %REC and MAXLINE in Experiment 1

		%REC		MAXLINE	
Source	*df*	*F*	η^2	*F*	η^2
Pattern x Mass	2,36	4.06*	0.33	2.70m.s.	0.13
Simple Effects of Mass					
At Inphase	2,36	9.31**	0.34	3.89*	0.18
1 kg vs. 3 kg	1,18	0.57	0.03	0.00	0.00
1 kg vs. 5 kg	1,18	14.58**	0.45	4.73*	0.21
3 kg vs. 5 kg	1,18	10.55**	0.37	10.28**	0.36
At Antiphase	2,36	0.14	0.01	0.17	0.01
Simple Effects of Pattern					
At 1 kg	1,18	1.45	0.08	1.10	0.06
At 3 kg	1,18	0.01	0.00	0.19	0.01
At 5 kg	1,18	6.79*	0.27	5.44*	0.23

Note. m.s. *marginally significant,* * $p < .05$, ** $p < .01$.

Table 3

Preferred Mean Movement and Breathing Frequency (Hz) and the Variable Error of Movement and Breathing Frequency (Hz) at Baseline in Experiment 2

	Mean (*SD*)	Variable Error (*SD*)
Movement Frequency		
0 kg	0.663 (0.079)	0.024 (0.010)
1 kg	0.661 (0.061)	0.018 (0.009)
3 kg	0.640 (0.057)	0.014 (0.005)
5 kg	0.623 (0.053)	0.018 (0.014)
Breathing Frequency		
Resting	0.238 (0.054)	0.027 (0.014)
Loaded		
0 kg	0.260 (0.049)	0.050 (0.020)
1 kg	0.281 (0.075)	0.049 (0.028)
3 kg	0.281 (0.075)	0.046 (0.027)
5 kg	0.298 (0.102)	0.062 (0.030)

Table 4

Decomposition of the Mass x Metronome Frequency Interaction for the Constant Error and Variable Error of Relative Phase Performance in Experiment 2

		Constant Error		Variable Error	
Source	*df*	*F*	η^2	*F*	η^2
Mass x Metronome Frequency	2,24	13.49***	0.53	4.14*	0.26
Simple Effects of Mass					
At 0.54 Hz	2,24	3.90*	0.25	0.92	0.07
1 kg vs. 3 kg	1,12	5.05*	0.30	0.31	0.03
1 kg vs. 5 kg	1,12	5.69*	0.32	1.91	0.14
3 kg vs. 5 kg	1,12	1.13	0.09	0.73	0.06
At 0.78 Hz	2,24	10.98***	0.48	5.72**	0.32
1 kg vs. 3 kg	1,12	31.63***	0.73	0.41	0.03
1 kg vs. 5 kg	1,12	14.04**	0.54	12.69**	0.51
3 kg vs. 5 kg	1,12	1.09	0.08	9.79**	0.45

Note. m.s.*marginally significant*, *$p < .05$, **$p < .01$, ***$p < .001$.

Table 5

Decomposition of the Mass x Metronome Frequency Interaction for the Cross Recurrence Quantification Analysis Measures %REC and MAXLINE in Experiment 2

		%REC		MAXLINE	
Source	*df*	*F*	η^2	*F*	η^2
Mass	2,24	0.72	0.06	4.49*	0.27
Mass x Metronome Frequency	2,24	14.29***	0.54	3.19$^{m.s.}$	0.21
Simple Effects of Mass					
At 0.54 Hz	2,24	7.09**	0.37	0.17	0.01
1 kg vs. 3 kg	1,12	7.87*	0.40	0.00	0.00
1 kg vs. 5 kg	1,12	8.70*	0.42	0.23	0.02
3 kg vs. 5 kg	1,12	1.63	0.12	0.81	0.06
At 0.78 Hz	2,24	9.00**	0.43	13.44***	0.53
1 kg vs. 3 kg	1,12	3.97$^{m.s.}$	0.25	2.54	0.18
1 kg vs. 5 kg	1,12	13.55**	0.53	31.40***	0.72
3 kg vs. 5 kg	1,12	6.50*	0.35	14.69**	0.55

Note. $^{m.s.}$*marginally significant,* $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

Table 6

Preferred Mean Movement and Breathing Frequency (Hz) and the Variable Error of Movement and Breathing Frequency (Hz) at Baseline in Experiment 3

	Mean (*SD*)	Variable Error (*SD*)
Movement Frequency		
Uncoupled	0.637 (0.101)	0.021 (0.006)
Coupled	0.540 (0.163)	0.026 (0.009)
Breathing Frequency		
Uncoupled		
Resting	0.252 (0.041)	0.034 (0.024)
Loaded	0.261 (0.079)	0.055 (0.033)
Coupled	0.540 (0.164)	0.037 (0.011)

Table 7

T-tests for Inphase and Antiphase Performance During Experimental Trials in Experiment 3 in which Movement Frequency and Breathing Frequency were Compared to Test-Values of 1.05 Hz, 1.20 Hz, and 1.35 Hz

		Movement Frequency	Breathing Frequency
Source	*df*	*t*	*t*
Inphase			
1.05 Hz	12	4.49**	5.06***
1.20 Hz	11	5.86***	3.56**
1.35 Hz	11	3.04*	2.22*
Antiphase			
1.05 Hz	11	4.02**	2.68*
1.20 Hz	11	3.50**	2.78*
1.35 Hz	10	3.54**	2.97*

Note. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .01$

Table 8

Analysis of Variance on the Dependent Measures Movement Frequency and Breathing Frequency in Experiment 3

		Movement Frequency		Breathing Frequency	
Source	*df*	*F*	η^2	*F*	η^2
Pattern	1,10	7.73^{*}	0.44	5.37^{*}	0.35
Frequency Plateau	6,60	277.33^{***}	0.97	268.66^{***}	0.96
0.45 Hz vs. 0.60 Hz	1,12	654.11^{***}	0.98	509.84^{***}	0.98
0.60 Hz vs. 0.75 Hz	1,12	567.71^{***}	0.98	750.18^{***}	0.98
0.75 Hz vs. 0.90 Hz	1,12	695.30^{***}	0.98	791.18^{***}	0.99
0.90 Hz vs. 1.05 Hz	1,11	708.55^{***}	0.99	341.88^{***}	0.98
1.05 Hz vs. 1.20 Hz	1,11	116.09^{***}	0.91	41.38^{***}	0.79
1.20 Hz vs. 1.35 Hz	1,10	9.24^{*}	0.48	10.09^{*}	0.50
Pattern x Frequency Plateau	6,60	5.24^{***}	0.34	4.57^{**}	0.31
Pattern x 1.20 Hz vs. 1.35 Hz	1,10	$4.46^{m.s.}$	0.31	$4.83^{m.s.}$	0.51

Note. $^{m.s.}$*marginally significant,* $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$; one participant could not complete the 1.05 Hz through 1.35 Hz plateaus; another participant could not complete the 1.35 Hz plateau.

Table 9

Attractor Reconstruction Parameters in Experiment 3

Prescribed Frequency (Hz)	Time Delay (τ)		Embedding Dimension	
	Used	Observed *M*(*SD*)	Used	Observed *M*(*SD*)
0.45	28	27.17(1.00)	5	3.87(0.59)
0.60	21	20.62(0.84)	5	3.85(0.55)
0.75	17	16.90(0.56)	5	3.92(0.59)
0.90	14	14.15(0.34)	5	3.75(0.58)
1.05	12	12.47(0.58)	5	4.24(0.67)
1.20	11	10.94(0.54)	5	4.27(0.69)
1.35	10	10.35(1.34)	5	4.55(1.06)

Table 10

Analysis of Variance on the Cross Recurrence Quantification Analysis Measures %REC and MAXLINE for Inphase and Antiphase Performance in Experiment 3

Source	*df*	%REC		MAXLINE	
		F	η^2	*F*	η^2
			Inphase		
Frequency Plateau	3,9	5.38*	0.64	1.40	0.32
Before Transition Plateau 1 vs. (Transition and After Transition Plateaus)	1,3	50.86**	0.94	4.43	0.60
Before Transition Plateau 2 vs. (Transition and After Transition Plateaus)	1,3	0.89	0.23	0.40	0.12
			Antiphase		
Frequency Plateau	3,18	19.31***	0.76	6.70**	0.53
Before Transition Plateau 1 vs. (Transition and After Transition Plateaus)	1,6	22.64**	0.79	11.05*	0.65
Before Transition Plateau 2 vs. (Transition and After Transition Plateaus)	1,6	36.64**	0.86	5.84*	0.49

Note. $^{*}p \leq .05$, $^{**}p < .01$, $^{***}p < .001$; Exclusions due to a lack of After Transition Plateau data: two participants from the inphase condition and one from the antiphase condition.

Table 11

Preferred Mean Movement and Breathing Frequency (Hz) and the Variable Error of Movement and Breathing Frequency (Hz) at Baseline in Experiment 4

	Mean (*SD*)	Variable Error (*SD*)
Movement Frequency	0.689 (0.087)	0.023 (0.010)
Breathing Frequency		
Resting	0.300 (0.109)	0.034 (0.019)
Loaded	0.283 (0.113)	0.067 (0.052)

Table 12

Analysis of Variance on the Cross Recurrence Quantification Analysis Measures %REC and MAXLINE in Experiment 4

Source	*df*	%REC		MAXLINE	
		F	η^2	*F*	η^2
Pattern	1,14	6.11*	0.30	3.82 m.s.	0.21
Feedback	2,28	24.45***	0.64	6.47**	0.32
No Feedback vs. Inphase Feedback	1,14	30.61***	0.69	8.68*	0.38
No Feedback vs. Antiphase Feedback	1,14	0.29	0.02	0.43	0.03
Inphase Feedback vs. Antiphase Feedback	1,14	43.23***	0.76	12.03**	0.46

Note. m.s. *marginally significant,* * $p < .05$, ** $p < .01$, *** $p < .001$.

FIGURE CAPTIONS

Figure 1. Lagged return plots depict the evolution of relative phase over a time delay (τ) for a representative larger-integer, complex ratio trial (5:3; left panel) and smaller-integer, simple ratio trial (3:1; right panel). The dashed line in each panel indicates the relative phase values for idealized ratio performance.

Figure 2. The motion equation for simulated comfortable (b/a = 1; solid line) and fast (b/a = 0.25; dashed line) frequencies. The detuning parameter $\Delta\omega = 0$. Attractors are indicated by the negatively-sloped zero crossings and repellors by the positively-sloped zero crossings.

Figure 3. The motion equation for no frequency detuning ($\Delta\omega = 0$; solid line) and negative frequency detuning ($\Delta\omega = -1$; dashed line). The coupling parameter b/a = 1. Attractors are indicated by the negatively-sloped zero crossings and repellors by the positively-sloped zero crossings.

Figure 4. A depiction of the predictions of the HKB model for inphase versus antiphase performance (left panels) and low versus high oscillation frequency (right panels) over several values of frequency asymmetry. Deviation of the predicted relative phase, ϕ, from the intended relative phase, ψ, and the variability of relative phase, $SD\phi$, are shown.

Figure 5. Predictions for the constant error (top panel) and variable error (bottom panel) of relative phase performance for inphase (solid line) and antiphase (dashed line) over several values of negative frequency asymmetry ($\Delta\omega$).

Figure 6. The task performed by participants.

Figure 7. Sample raw data (top panels), phase portraits (middle panels), and continuous relative phase (bottom panel) calculated from those phase portraits for a single participant who was performing the inphase pattern. The top and middle panels include data for movement (left panels) and breathing (right panels).

Figure 8. The constant error (top panel) and variable error (bottom panel) of relative phase performance as a function of pattern (inphase: solid line; antiphase: dashed line) and mass. Error bars correspond to the standard error of each condition.

Figure 9. Three dimensions of the reconstructed movement (top panels) and breathing (bottom panels) attractors for a single participant in the largest (left panels) and smallest (right panels) frequency asymmetry conditions. The data are from an inphase trial. The time delay (τ) was 24 data points.

Figure 10. Cross recurrence plots for a single participant in the largest (left panel) and smallest (right panel) frequency asymmetry conditions. The data are from an inphase trial. Points were considered cross-recurrent if they were within 21% of the mean distance of the reconstructed attractor. For this participant, the cross recurrence measures were lower at the largest frequency asymmetry (%REC = 3.87; MAXLINE = 462) than at the smallest frequency asymmetry (%REC = 5.20; MAXLINE = 569).

Figure 11. %REC (top panel) and MAXLINE (bottom panel) as a function of pattern (inphase: solid line; antiphase: dashed line) and mass. Error bars correspond to the standard error of each condition.

Figure 12. Predictions for the constant error (top panel) and variable error (bottom panel) of relative phase performance for slow (circles) and fast (triangles) frequencies over several values of negative frequency asymmetry ($\Delta\omega$).

Figure 13. The constant error (top panel) and variable error (bottom panel) of inphase performance as a function of metronome frequency (0.54 Hz: circles; 0.78 Hz: triangles) and mass. Error bars correspond to the standard error of each condition.

Figure 14. %REC (top panel) and MAXLINE (bottom panel) for inphase performance as a function of metronome frequency (0.54 Hz: circles; 0.78 Hz: triangles) and mass. Error bars correspond to the standard error of each condition.

Figure 15. Mean movement (top panels) and breathing (bottom panels) frequencies (solid lines) for experimental trials as a function of frequency plateau and relative phase (inphase: left panels; antiphase: right panels). Prescribed frequencies are depicted as circles. Gray areas represent 95% confidence intervals.

Figure 16. Continuous relative phase as a function of frequency plateau and starting relative phase (inphase: top panels; antiphase: bottom panels) for sample trials in which transitions were observed. Transitions were from stable relative phases (inphase: 0°; antiphase: 180°) to phase wrapping and/or intermittency. A few examples of phase wrapping and intermittency are labeled. To better observe phase wrapping, continuous relative phase is displayed between -360° and 360°. The data are zero-padded until the first relative phase calculation.

Figure 17. %REC (top panel) and MAXLINE (bottom panel) as a function of frequency plateau and the starting relative phase (inphase: solid lines; antiphase: dashed lines) for trials in which transitions were observed. Note the decrease in both measures at the transition plateau. Error bars correspond to the standard error of each condition.

Figure 18. Three dimensions of the reconstructed movement (top panels) and breathing (bottom panels) attractors for a single participant before (0.75 Hz: left panels) and after (1.35 Hz: right panels) a transition from antiphase to phase wrapping and intermittency. The time delays (τ) used at 0.75 Hz and 1.35 Hz were 17 data points and 10 data points, respectively. For this participant, %REC dropped from 2.97 to 0.57 and MAXLINE dropped from 294 to 67 from before to after the transition.

Figure 19. In the ball display, ball motion was controlled by breathing (labeled B) or movement (labeled M). Vertical dashed lines represent the total excursion of the balls. When feedback orientation was reversed, the locations of the max inhalation and max exhalation were reversed.

Figure 20. The constant error (top panel) and variable error (bottom panel) of relative phase performance as a function of pattern (inphase: filled bars; antiphase: open bars) and feedback condition. Error bars correspond to the standard error of each condition.

Figure 21. %REC (top panel) and MAXLINE (bottom panel) as a function of pattern (inphase: filled bars; antiphase: open bars) and feedback condition. Error bars correspond to the standard error of each condition.

Figure 22. Cross recurrence plots for a single participant who performed the antiphase pattern with inphase feedback (left panel) and antiphase feedback (right panel). Points were considered cross-recurrent if they were within 21% of the mean distance of the reconstructed attractor. For this participant, the cross recurrence measures were lower with inphase (%REC: 2.64; MAXLINE: 206) than antiphase (%REC: 4.95; MAXLINE: 545) feedback.

APPENDIX A

HUMAN PARTICIPANTS APPROVAL

ASU ARIZONA STATE UNIVERSITY
RESEARCH AND ECONOMIC AFFAIRS

Office of Research Integrity and Assurance

To:	Polemnia Amazeen TC
From:	Mark Roosa, Chair Soc Beh IRB
Date:	08/31/2009
Committee Action:	**Exemption Granted**
IRB Action Date:	08/31/2009
IRB Protocol #:	0908004281
Study Title:	Motor-Respiratory Coordination

The above-referenced protocol is considered exempt after review by the Institutional Review Board pursuant to Federal regulations, 45 CFR Part 46.101(b)(2) .

This part of the federal regulations requires that the information be recorded by investigators in such a manner that subjects cannot be identified, directly or through identifiers linked to the subjects. It is necessary that the information obtained not be such that if disclosed outside the research, it could reasonably place the subjects at risk of criminal or civil liability, or be damaging to the subjects' financial standing, employability, or reputation.

You should retain a copy of this letter for your records.

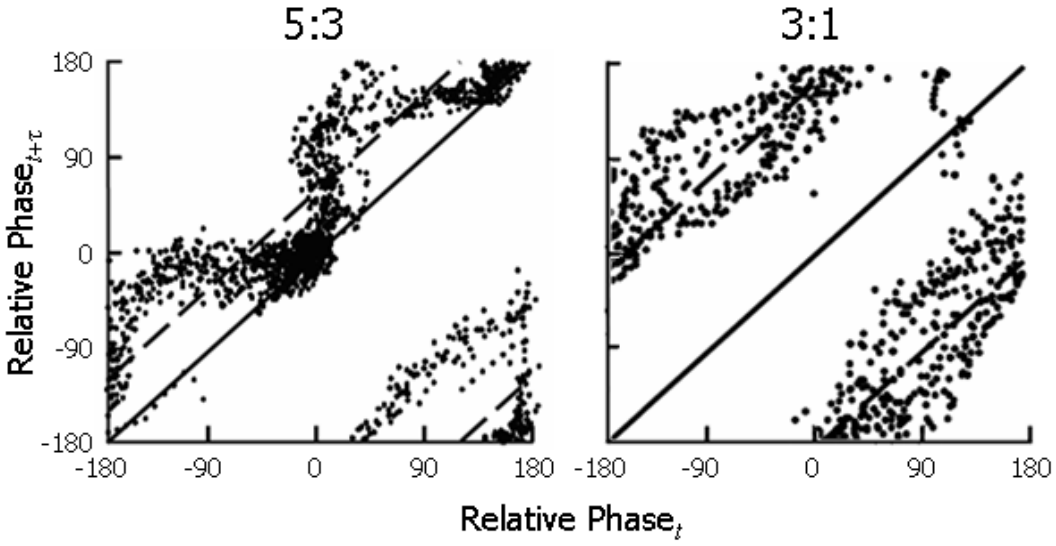
5:3
3:1
180
90
0
-90
-180
Relative Phase$_{t+\tau}$
-180
-90
0
90
180
Relative Phase$_t$

Fig. 1

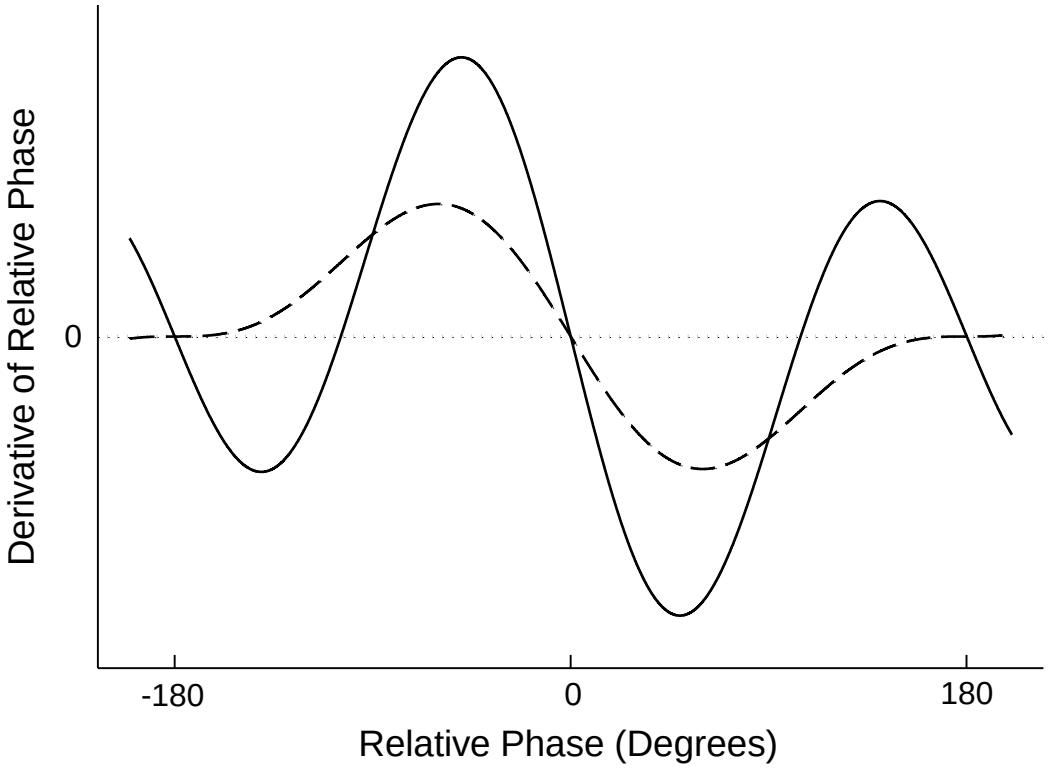
Derivative of Relative Phase
0
-180
0
180
Relative Phase (Degrees)

Fig. 2.

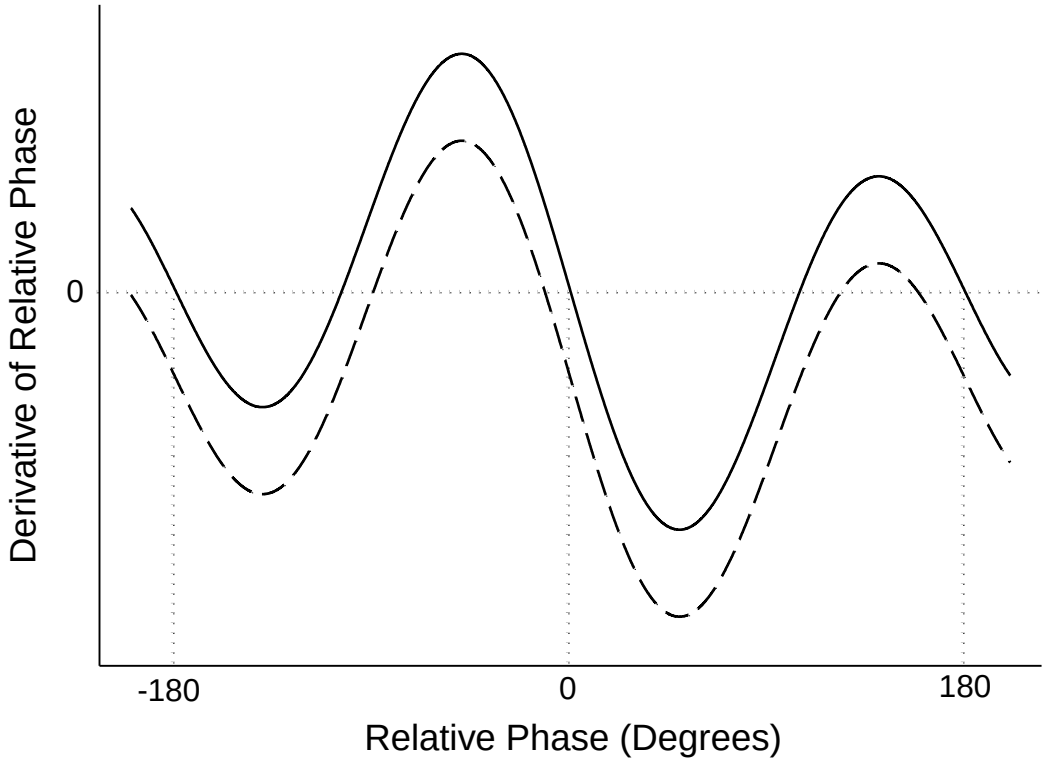
Derivative of Relative Phase
0
-180
0
180
Relative Phase (Degrees)

Fig. 3.

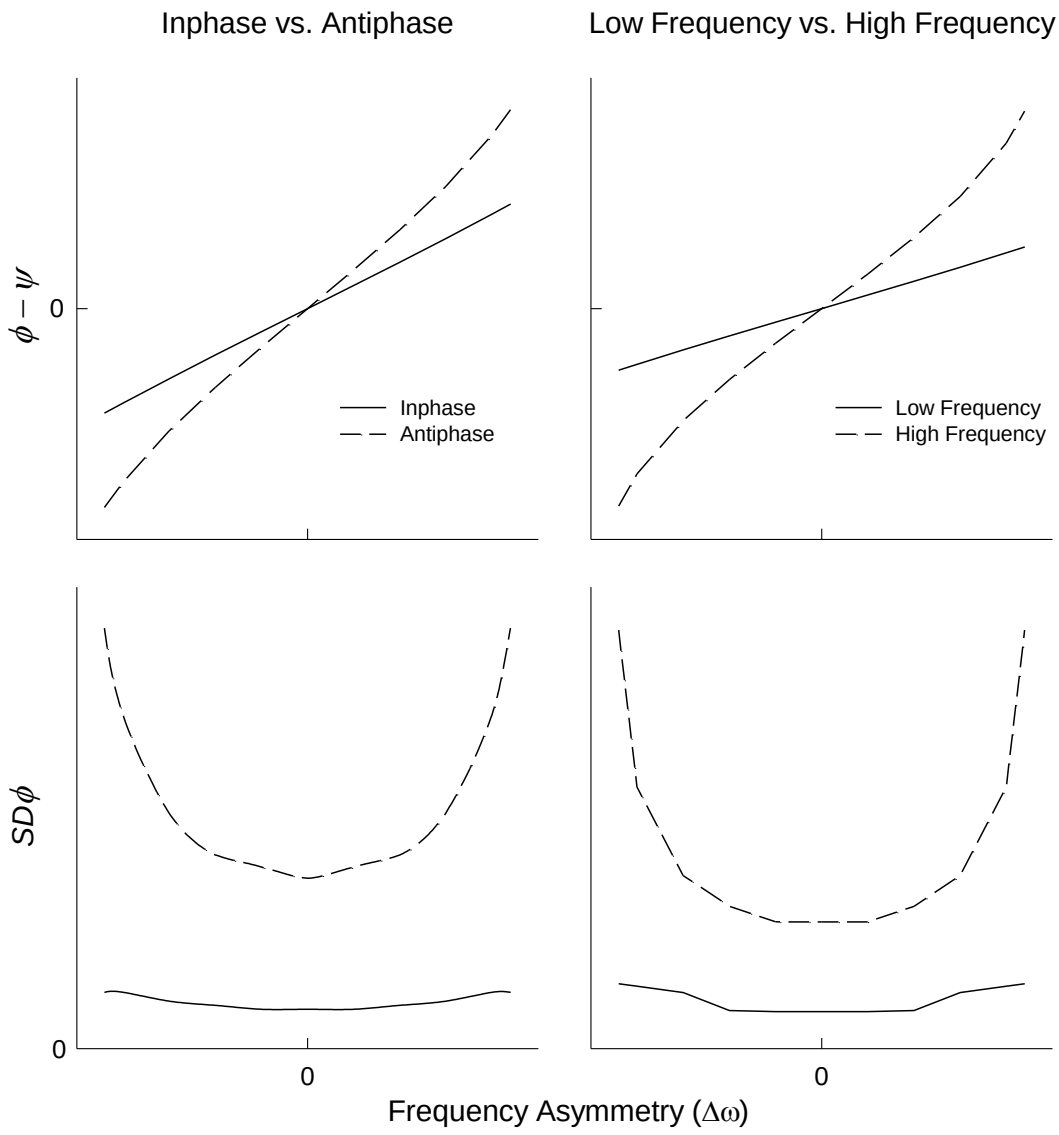
Inphase vs. Antiphase
Low Frequency vs. High Frequency
$\phi - \psi$
0
Inphase
Antiphase
Low Frequency
High Frequency
$SD\phi$
0
0
0
Frequency Asymmetry ($\Delta\omega$)

Fig. 4.

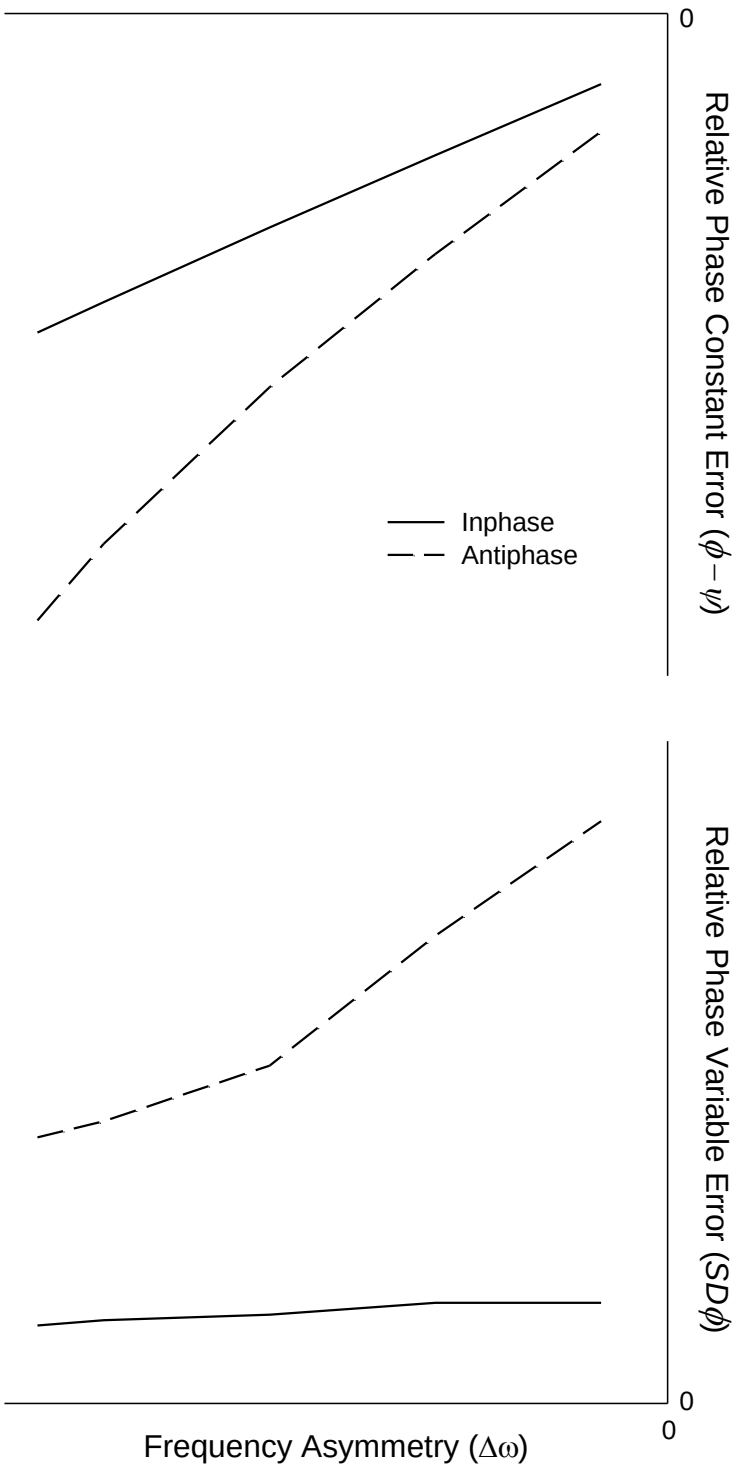
0
Relative Phase Constant Error ($\phi - \psi$)
Inphase
Antiphase
Relative Phase Variable Error ($SD\phi$)
0
0
Frequency Asymmetry ($\Delta\omega$)

Fig. 5.

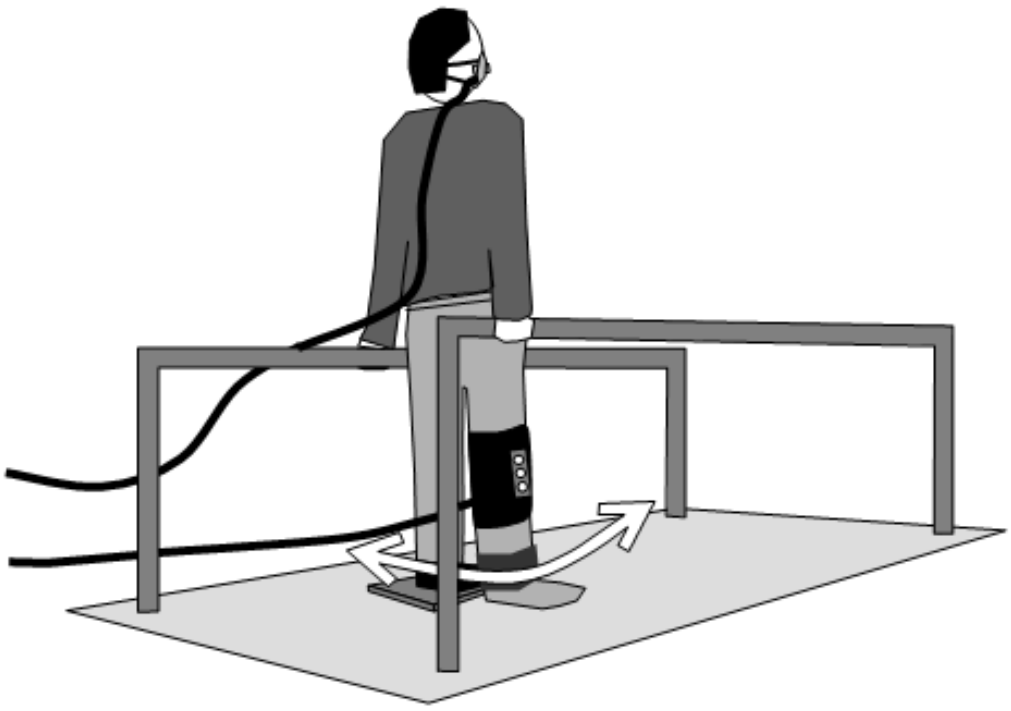

Fig. 6.

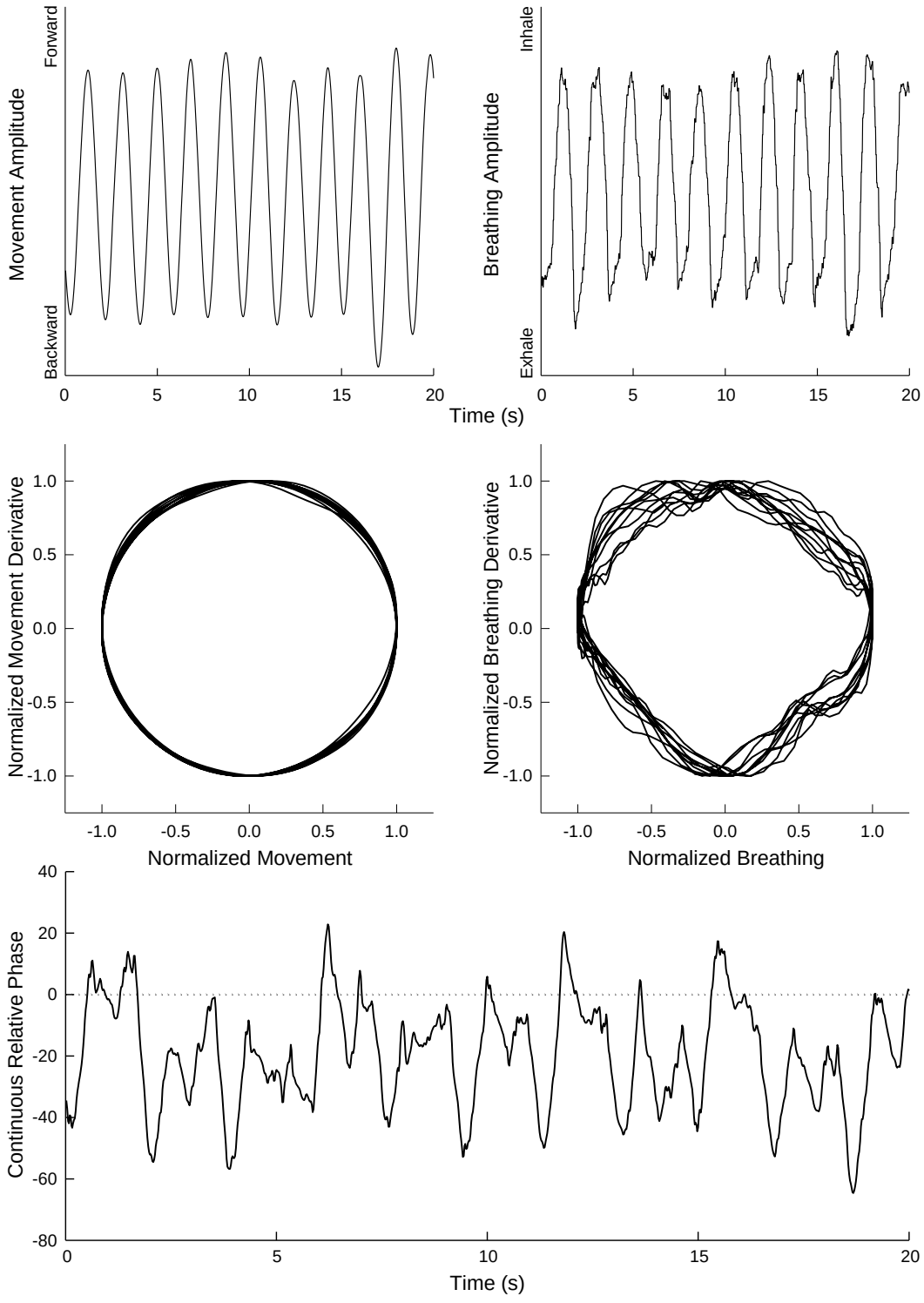
Movement Amplitude
Forward
Backward
Breathing Amplitude
Inhale
Exhale
0
5
10
15
20
Time (s)
Normalized Movement Derivative
1.0
0.5
0.0
-0.5
-1.0
Normalized Movement
Normalized Breathing Derivative
Normalized Breathing
Continuous Relative Phase
40
20
0
-20
-40
-60
-80
Time (s)

Fig. 7.

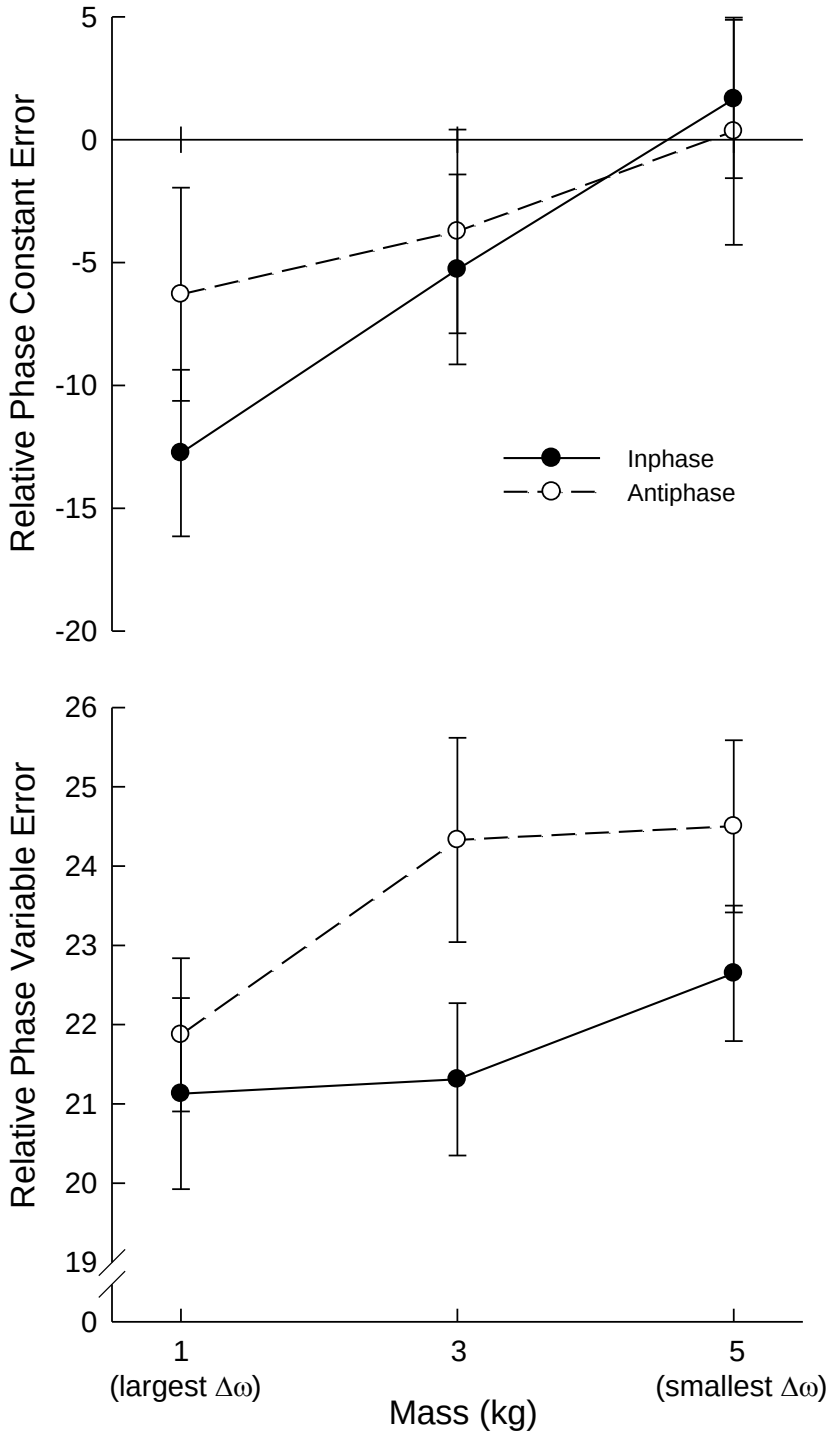
Relative Phase Constant Error
5
0
-5
-10
-15
-20
Inphase
Antiphase
Relative Phase Variable Error
26
25
24
23
22
21
20
19
0
1
(largest Δω)
3
5
(smallest Δω)
Mass (kg)

Fig. 8.

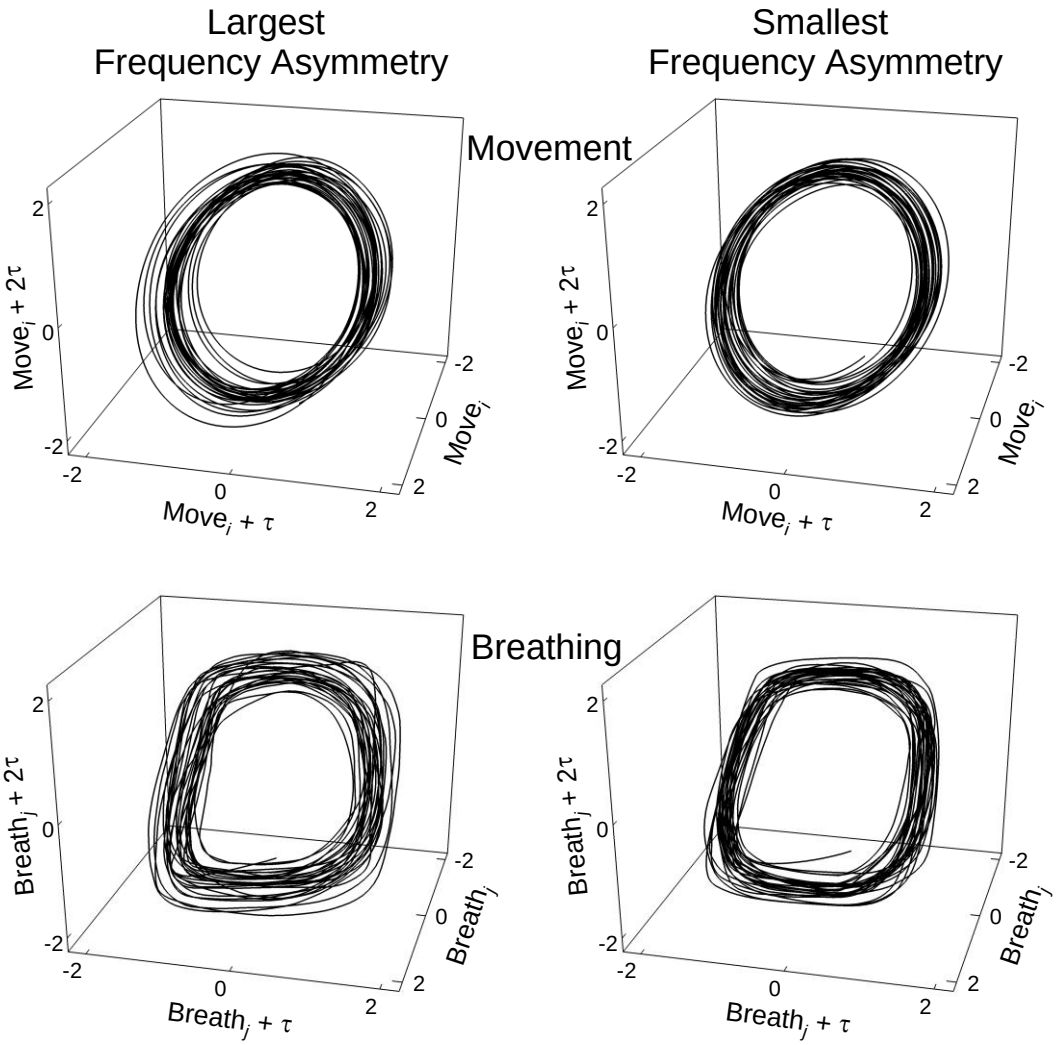
Largest
Frequency Asymmetry
Smallest
Frequency Asymmetry
Movement
Breathing
Move$_i$ + 2τ
Move$_i$ + τ
Move$_i$
Breath$_j$ + 2τ
Breath$_j$ + τ
Breath$_j$
2
0
-2

Fig. 9.

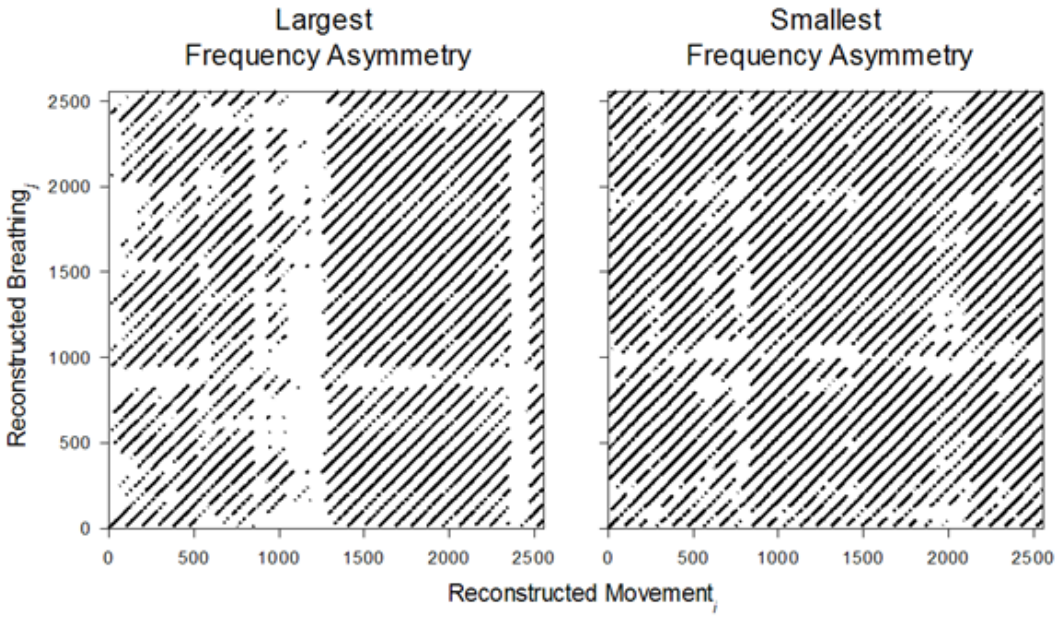
Largest
Frequency Asymmetry
Smallest
Frequency Asymmetry
Reconstructed Breathing$_i$
Reconstructed Movement$_i$
0
500
1000
1500
2000
2500

Fig. 10.

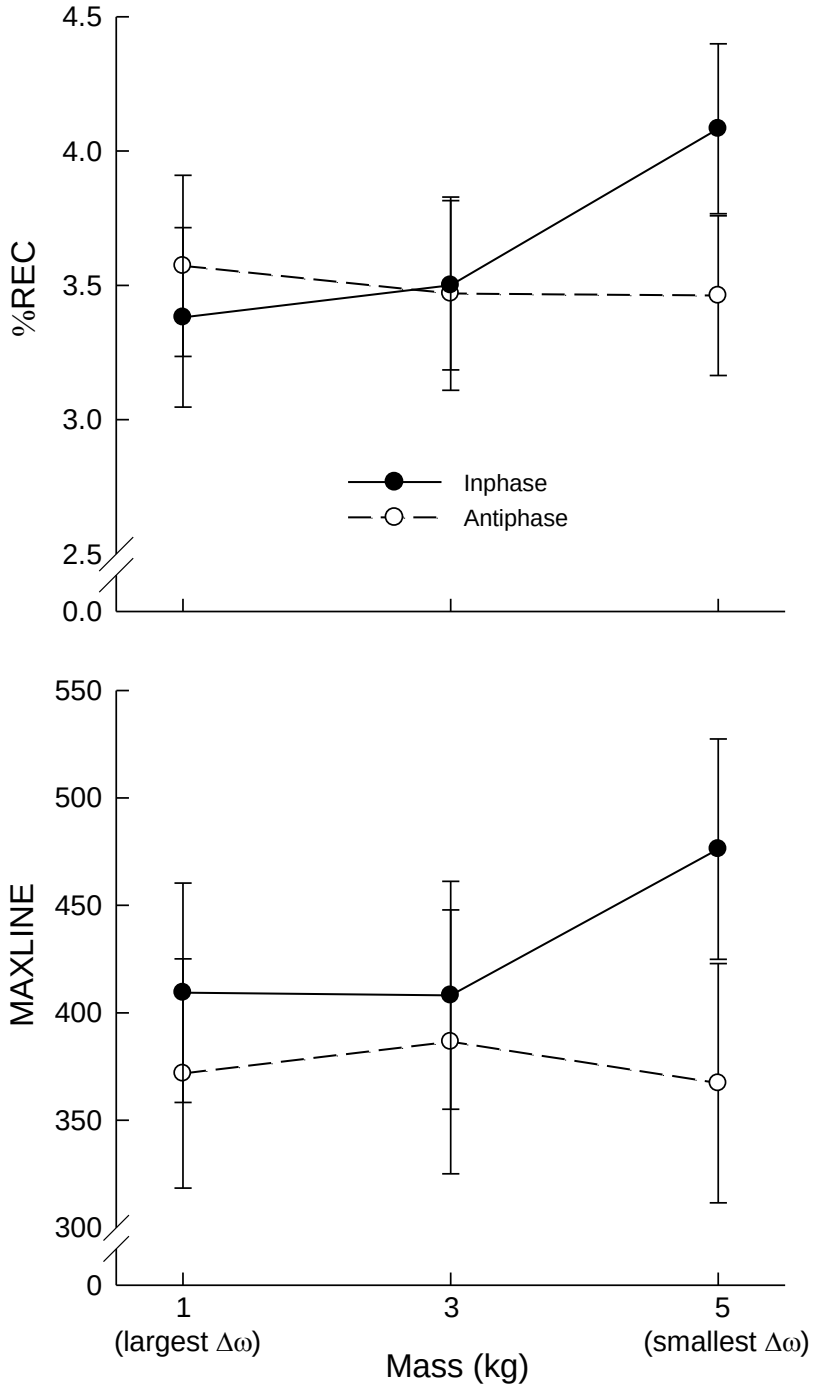
4.5
4.0
3.5
3.0
2.5
0.0
%REC
Inphase
Antiphase
550
500
450
400
350
300
0
MAXLINE
1
(largest Δω)
3
5
(smallest Δω)
Mass (kg)

Fig. 11.

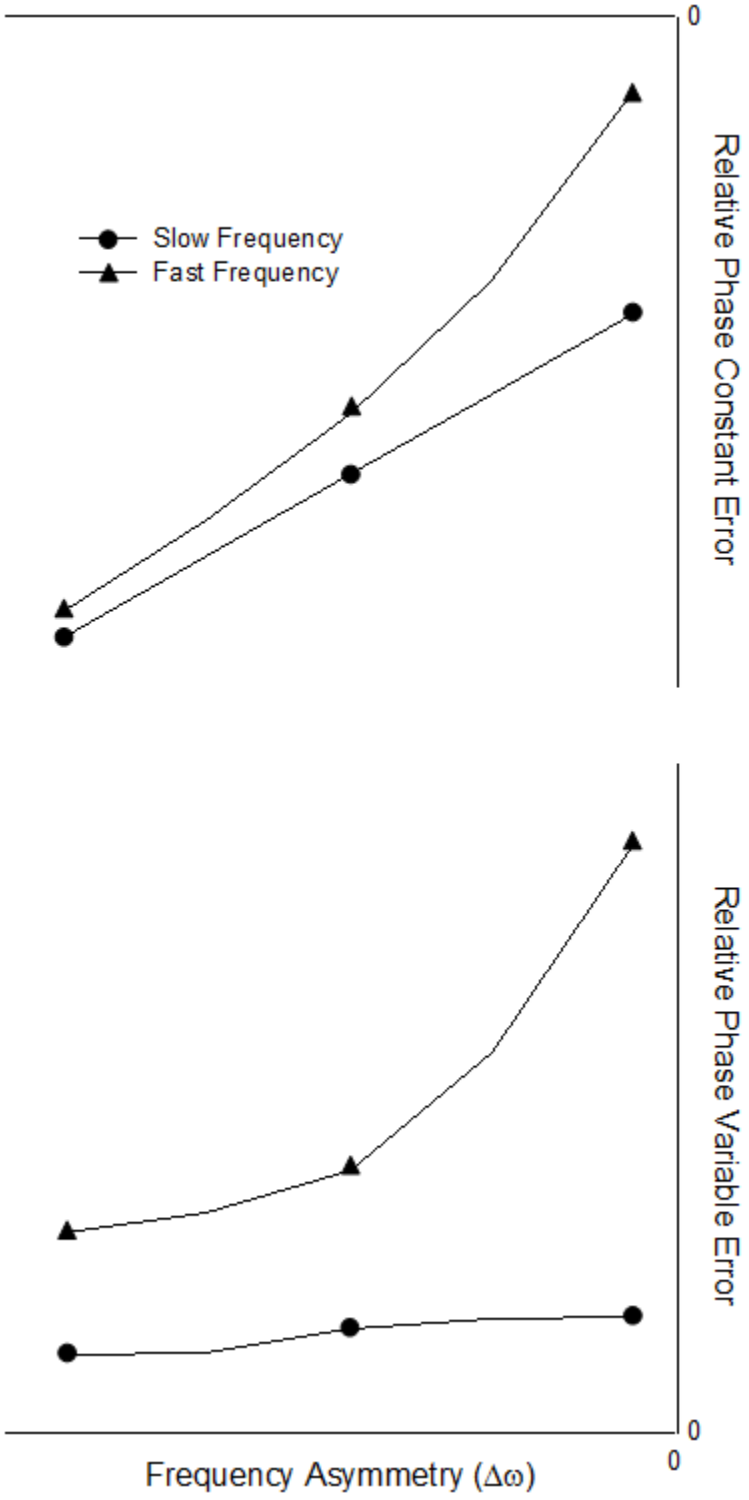
Slow Frequency
Fast Frequency
Relative Phase Constant Error
0
Relative Phase Variable Error
0
0
Frequency Asymmetry (Δω)

Fig. 12.

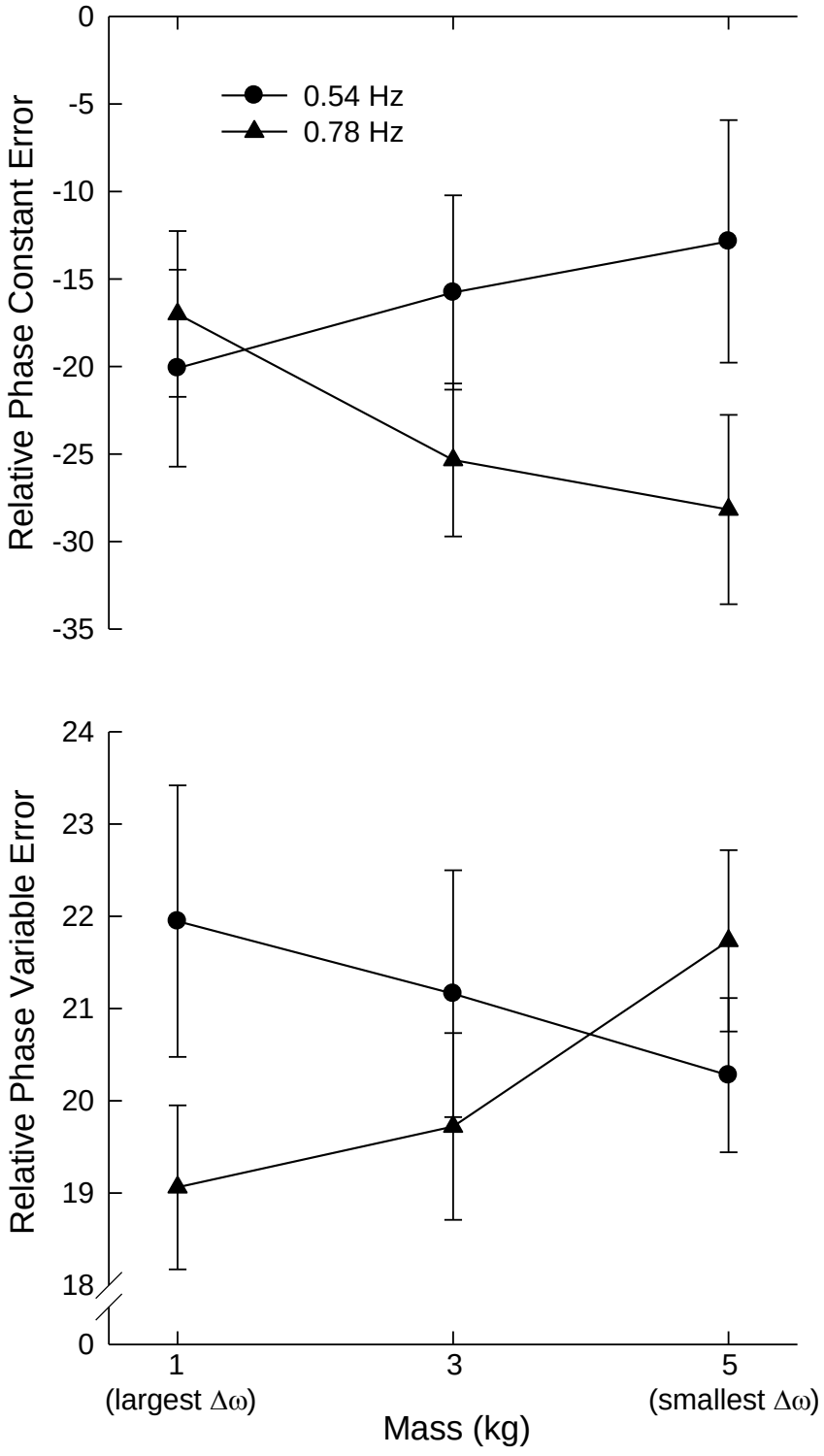
0
-5
-10
-15
-20
-25
-30
-35
Relative Phase Constant Error
0.54 Hz
0.78 Hz
24
23
22
21
20
19
18
0
Relative Phase Variable Error
1
(largest Δω)
3
5
(smallest Δω)
Mass (kg)

Fig. 13.

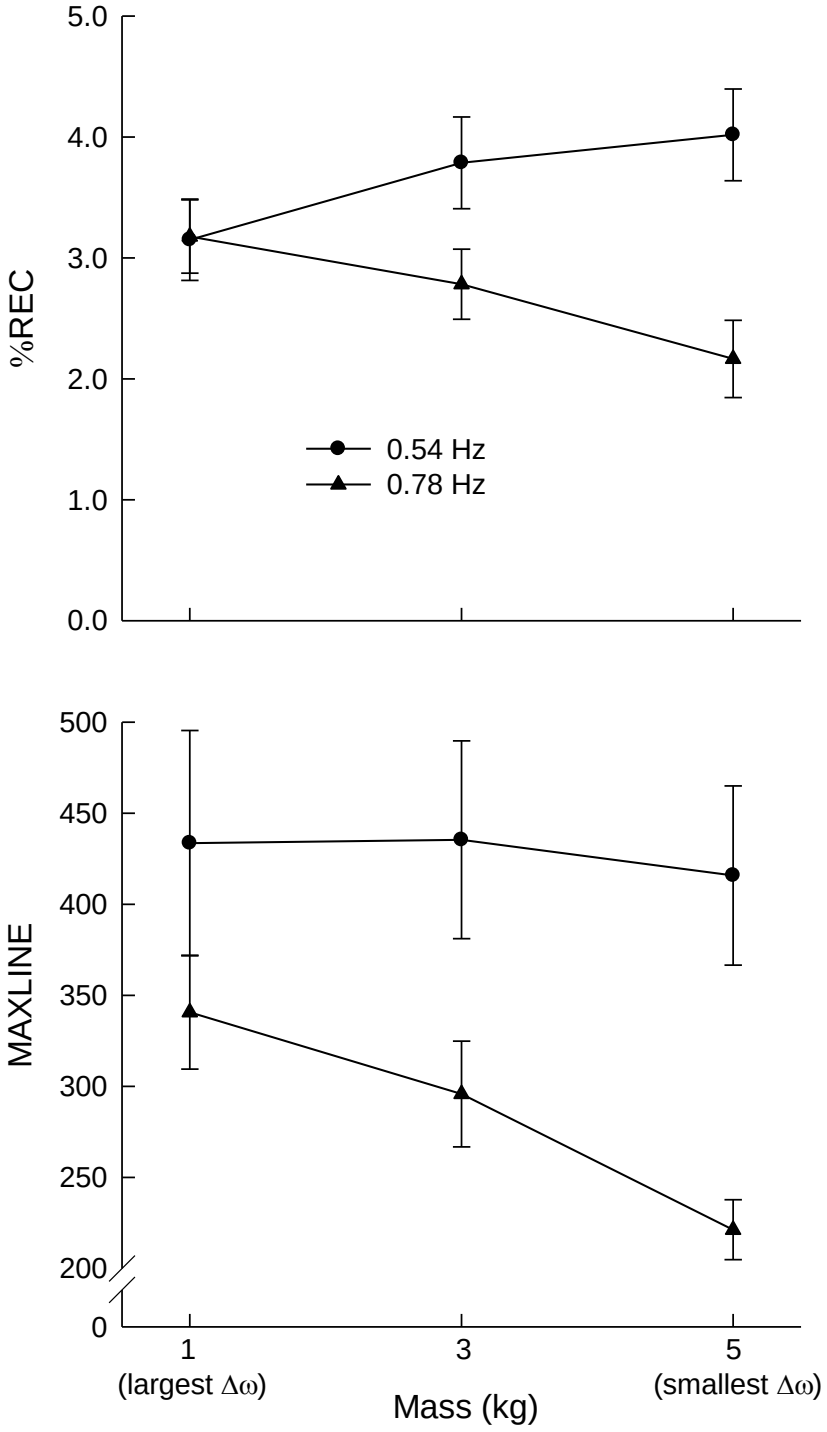
5.0
4.0
3.0
2.0
1.0
0.0
%REC
0.54 Hz
0.78 Hz
500
450
400
350
300
250
200
0
MAXLINE
1
(largest Δω)
3
5
(smallest Δω)
Mass (kg)

Fig. 14.

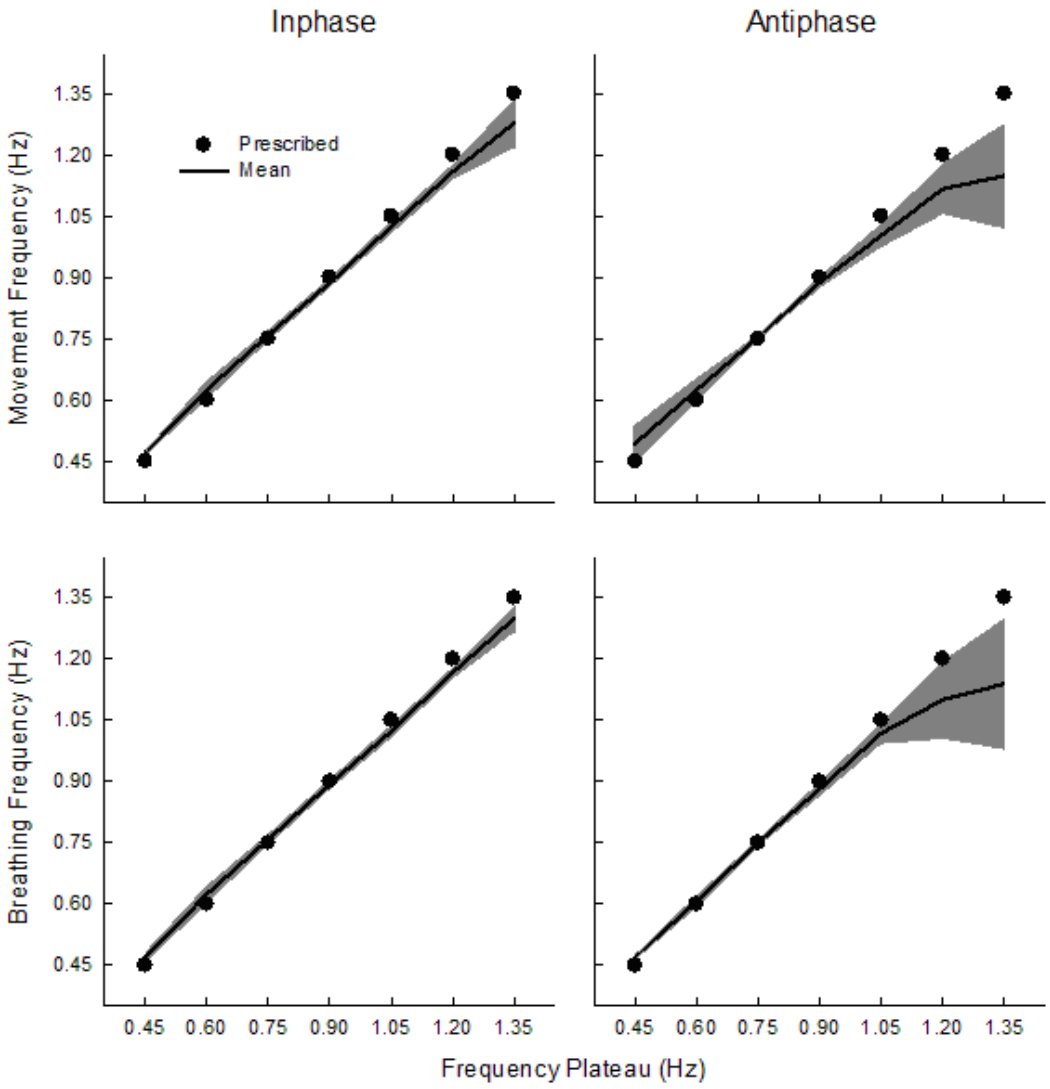
Inphase
Antiphase
Prescribed
Mean
Movement Frequency (Hz)
Breathing Frequency (Hz)
1.35
1.20
1.05
0.90
0.75
0.60
0.45
0.45 0.60 0.75 0.90 1.05 1.20 1.35
Frequency Plateau (Hz)

Fig. 15.

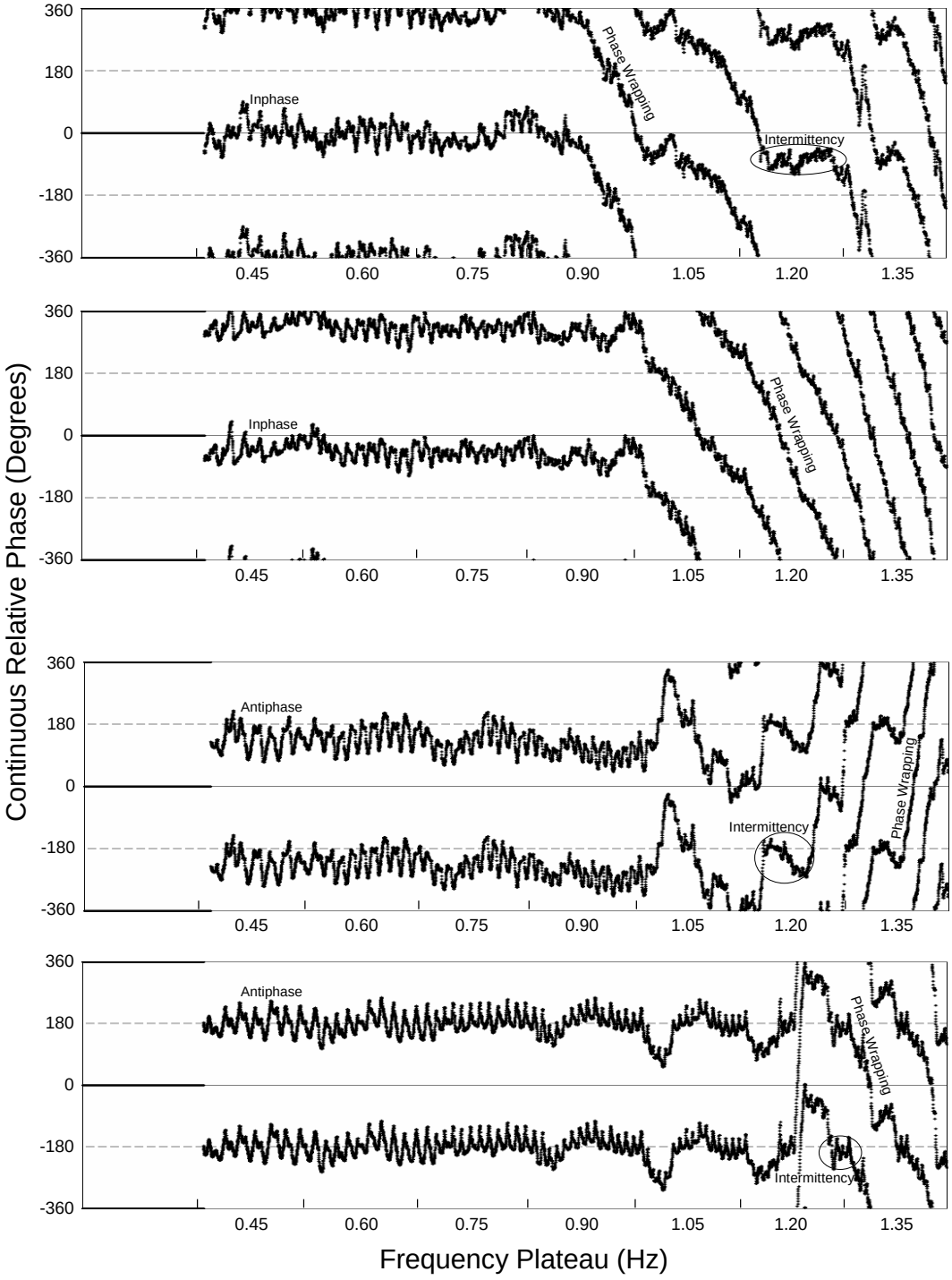
Continuous Relative Phase (Degrees)
360
180
0
-180
-360
0.45
0.60
0.75
0.90
1.05
1.20
1.35
Inphase
Phase Wrapping
Intermittency
Antiphase
Frequency Plateau (Hz)

Fig. 16.

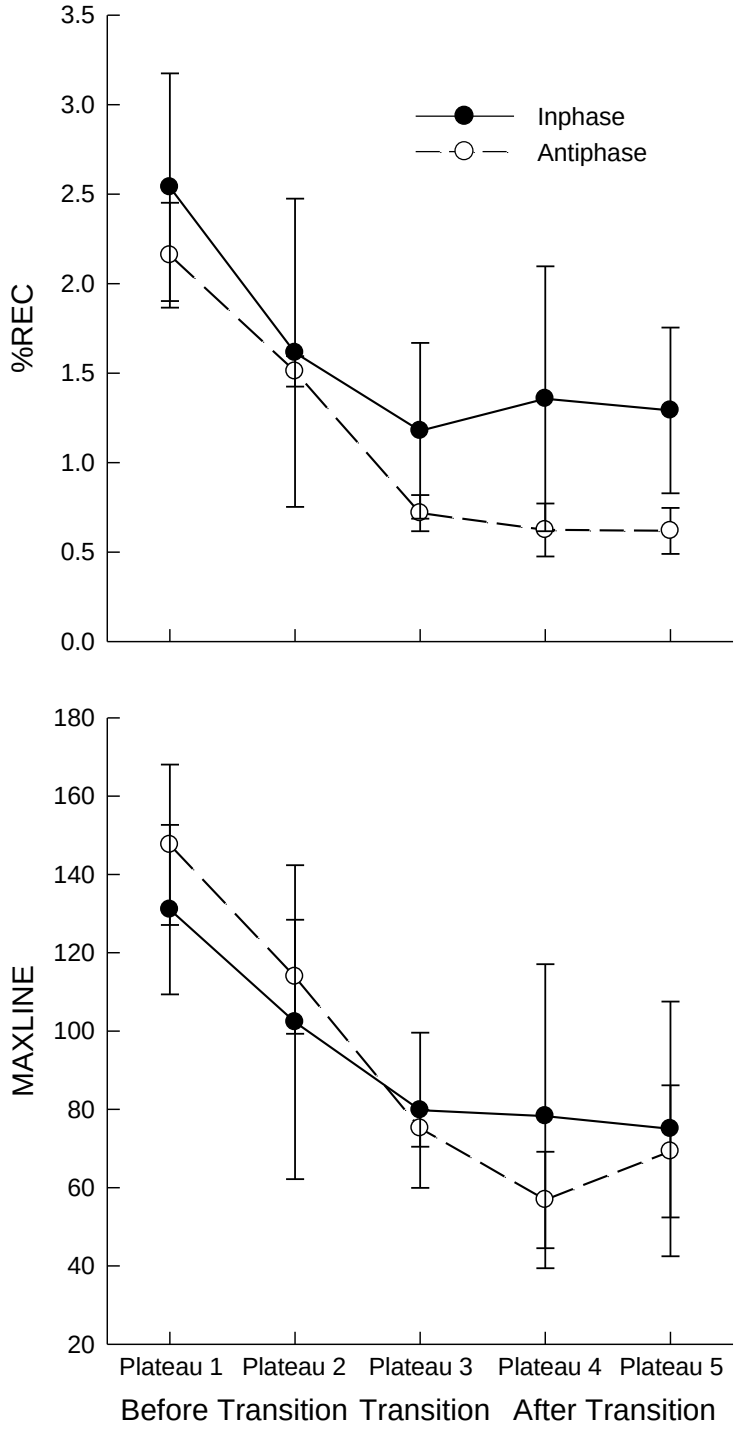
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
%REC
Inphase
Antiphase
180
160
140
120
100
80
60
40
20
MAXLINE
Plateau 1
Plateau 2
Plateau 3
Plateau 4
Plateau 5
Before Transition
Transition
After Transition

Fig. 17.

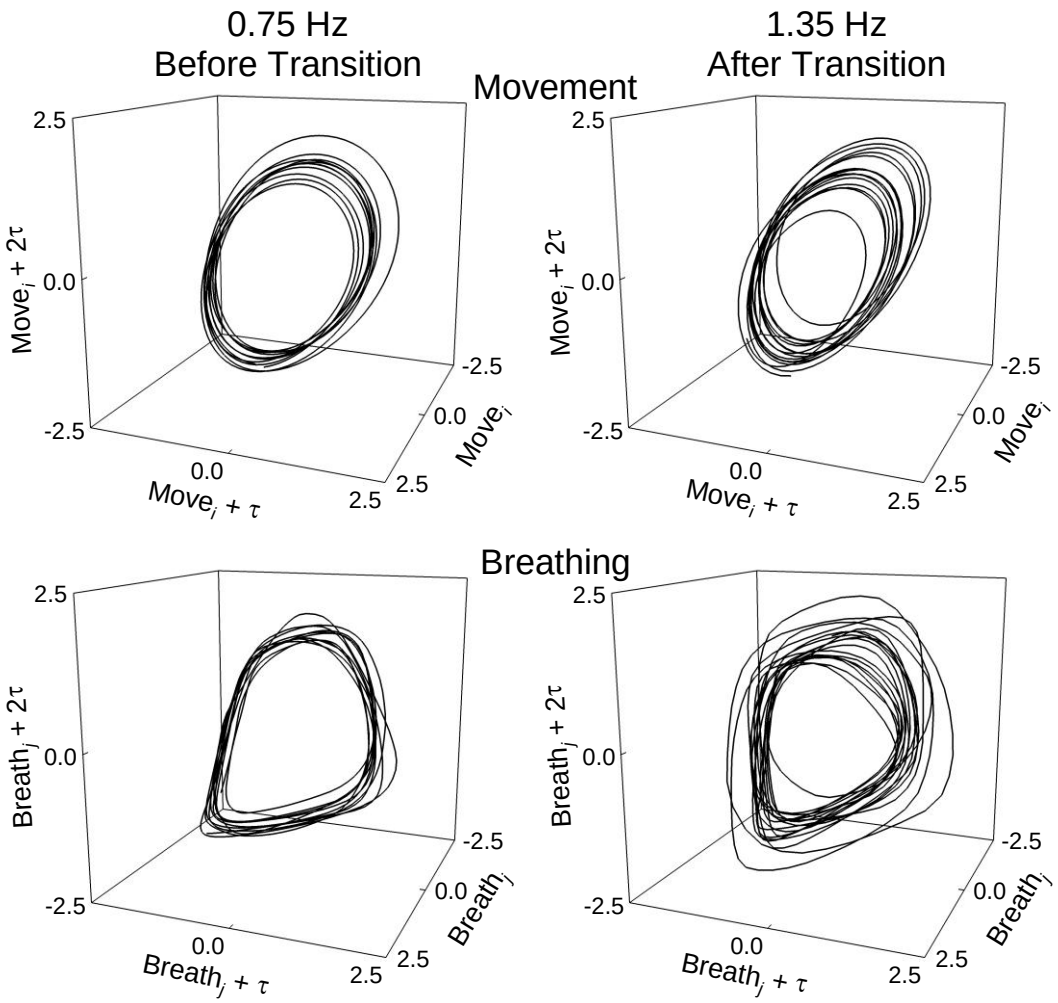
0.75 Hz
Before Transition
1.35 Hz
After Transition
Movement
Breathing
2.5
0.0
-2.5
Move$_i$ + 2τ
Move$_i$ + τ
Move$_j$
Breath$_j$ + 2τ
Breath$_j$ + τ
Breath$_j$

Fig. 18.

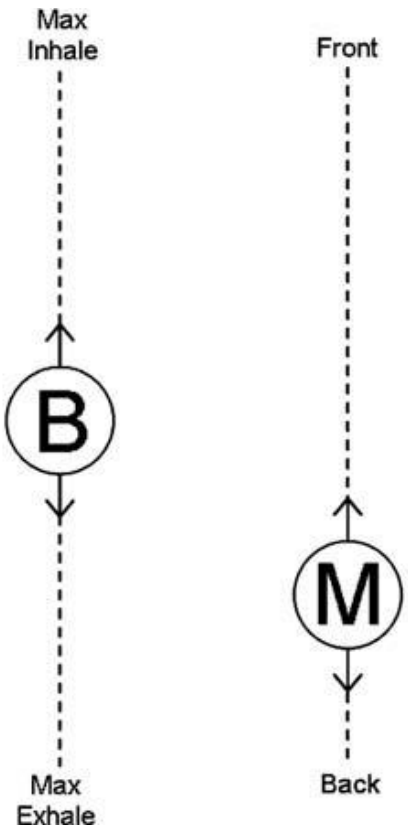

Fig. 19.

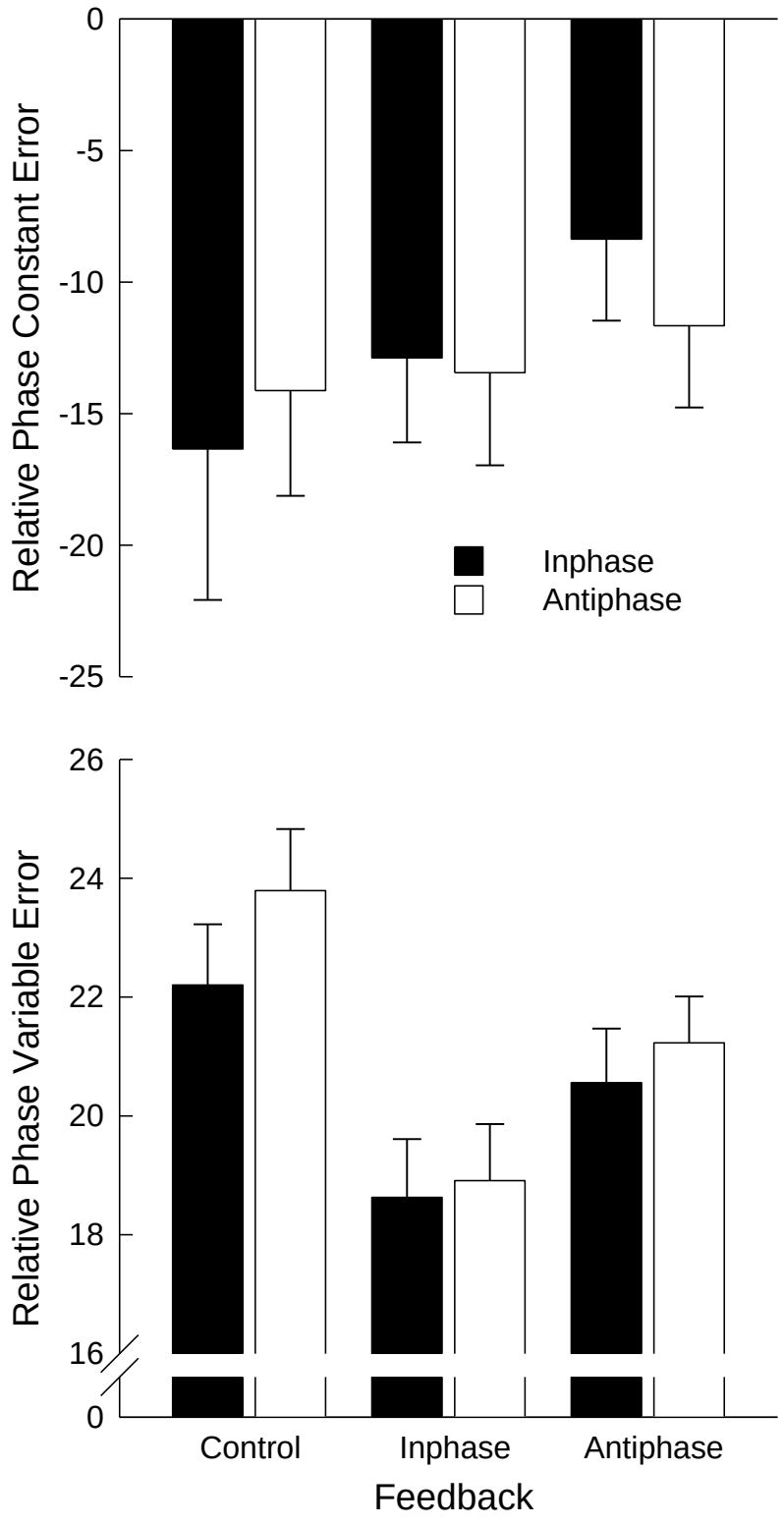
0
-5
-10
-15
-20
-25
Relative Phase Constant Error
Inphase
Antiphase
26
24
22
20
18
16
0
Relative Phase Variable Error
Control
Inphase
Antiphase
Feedback

Fig. 20.

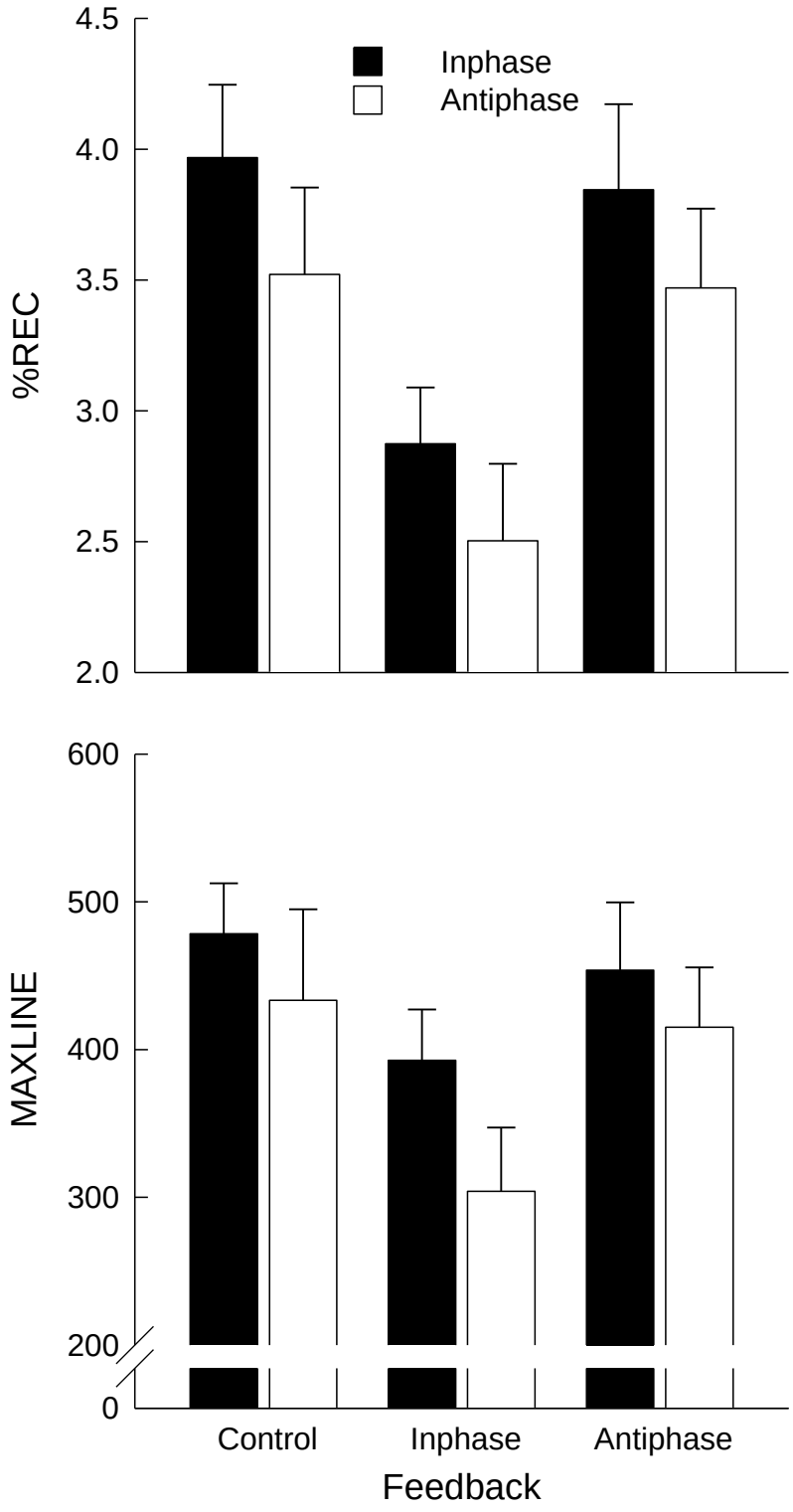
4.5
4.0
3.5
3.0
2.5
2.0
%REC
Inphase
Antiphase
600
500
400
300
200
0
MAXLINE
Control
Inphase
Antiphase
Feedback

Fig. 21.

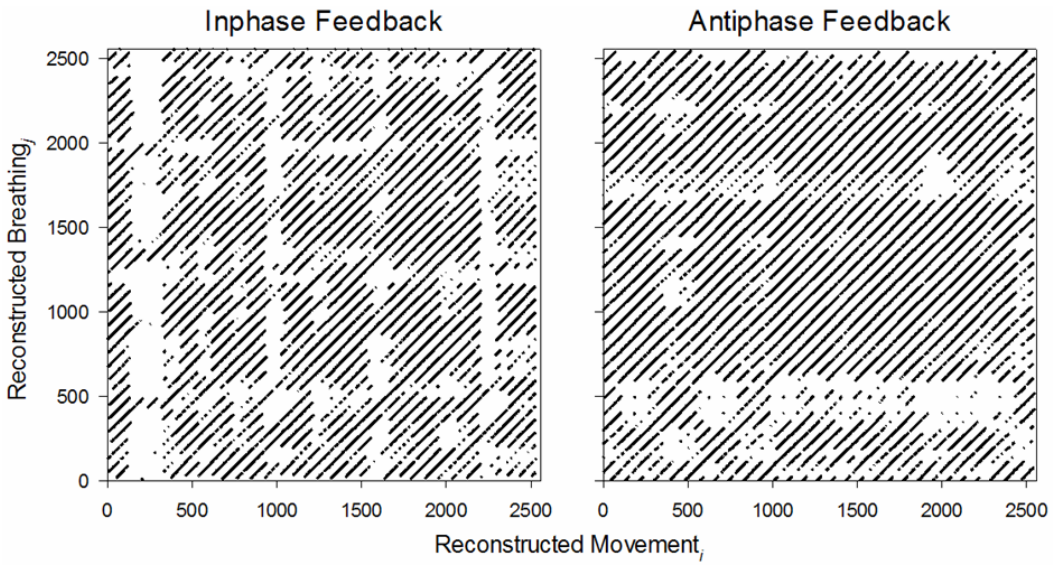
Inphase Feedback
Antiphase Feedback
Reconstructed Breathing$_j$
Reconstructed Movement$_i$
0
500
1000
1500
2000
2500

Fig. 22.